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EXPERIMENTAL STUDIES OF MIMICRY IN SOME NORTH AMERICAN BUTTERFLIES

PART II. *BATTUS PHILENOR* AND *PAPILIO TROILUS*, *P. POLYXENES* AND *P. GLAUCUS*[1]

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INTRODUCTION

Battus philenor (Linné) and its presumed mimics comprise a less frequently cited and more complex case of possible mimicry in North American butterflies than that of the well known Monarch and Viceroy. Edwards (1884) noted that Theodore L. Mead offered the suggestion that *B. philenor* is distasteful to birds, because he had noticed its strong, disagreeable scent. Mead thought that the unpalatability of *B. philenor* would serve to protect other black species flying with it. Edwards also stated that *B. philenor* is known to fly in company with *P. troilus* Linné, *P. polyxenes* (Fabricius), and the black female form of *P. glaucus* Linné, which hereafter will be called *P. glaucus* and will mean only the black form, unless otherwise noted.

A more elaborate hypothesis was offered by Poulton (1909) to account for the large number of apparent mimics of *B. philenor*. He suggested that the acceptability of these butterflies to predators might range from unpalatable to palatable, with *B. philenor* (model) the least palatable. According to Poulton, the most similar mimic of *B. philenor* is *P. troilus*, followed by *P. polyxenes*, *P. glaucus*, *Limenitis astyanax* (Fabricius) and finally the female of *Speyeria diana* (Cramer), in a series of decreasing resemblance and increasing palatability. Poulton tentatively called *P. troilus*, *P. polyxenes*, and *P. glaucus* primary mimics; *L. astyanax* a secondary mimic of the three *Papilios;* and the female of *S. diana* a tertiary mimic of *L. astyanax*. He found that *P. troilus*, *P. polyxenes*, *P. glaucus*, and *L. astyanax* resembled each other more closely than any of them resembled *B. philenor*. He suggested that they are Müllerian mimics, all somewhat unpalatable, but that *P. troilus* is the least palatable and *L. astyanax* the most. He considered the female of *S. diana* a Batesian mimic which is palatable

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to predators. Punnet (1915) thought that Poulton's hypothesis was unduly complicated, in the absence of experimental data to support or deny it, and he doubted that this case of mimicry actually existed. This unsettled controversy on the status of *B. philenor* and its presumed mimics thus offered an opportunity to investigate possible mimicry.

This second paper in a series of three describes further experiments with Florida Scrub Jays, *Cyanocitta coerulescens coerulescens* (Bosc), as caged predators and deals with mimicry in the *B. philenor* complex. The present experimental series, carried out at the Archbold Biological Station near Lake Placid, Florida, is a continuation of the first series which concerned mimicry in the Monarch and Viceroy butterflies. The same birds were used in both series, with the exception of one bird omitted in this series. The materials and methods used in the present paper have been described in an earlier paper (Brower, 1958).

Geographic Distribution and Sources of Butterflies

The following model and mimics were used in the course of these experiments: *B. philenor* (model) and *P. troilus, P. polyxenes,* and *P. glaucus* (mimics). Because of the difficulties involved in obtaining *L. astyanax* and *S. diana* while these experiments were in progress, possible mimicry in these two species was not investigated. The same species of non-mimetic butterfly (*P. glaucus,* yellow female and male) was used in this series as in the earlier series on the Monarch and Viceroy.

Because of the predominantly black color of *P. palamedes* (Drury), the other non-mimetic butterfly used in the previous series, this species was largely omitted from the second series, lest it be confused by the experimental birds with the black models and mimics to be tested. However, the trials in which *P. palamedes* was used as the non-mimetic butterfly, in couplet with a black model or mimic, showed that this precaution was unnecessary. The response to *P. palamedes* by the experimental birds in those trials was as follows: E-1, E-2, and E-3 each ate eight out of eight. The birds therefore apparently did discriminate *P. palamedes* from the model and mimics and responded to it just as they did in Part I. The basis of discrimination of *P. palamedes* by the birds may be the yellow stripe on the underside of the hind-wing and/or the two yellow stripes on the abdomen which are absent in the model and mimics. Further experiments are necessary to determine whether this is the case.

The distribution of *B. philenor* is from central New England, where it is rare, west through southern Ontario, Michigan, Wisconsin, and Nebraska to the coast of California, and south through Florida, Texas and Mexico. Although quantitative studies of the relative abundance of mimics and models were not made, field collecting for the present experiments indicated that *B. philenor* was scarce and local in south-central Florida in the spring of 1956. However, it is possible that the Florida Scrub Jays used as caged predators in the experiments could have encountered *B. philenor* in the wild. The range of *P. troilus* is somewhat greater than that of its supposed model. It occurs in southern Canada, south through Florida and Texas, and it was abundant in the vicinity of Lake Placid in the spring of 1956. Collecting showed that *P. polyxenes* was less common than *P. troilus* but more common than *B. philenor* in south-central Florida at that time. *P. polyxenes* occurs from New Brunswick to Manitoba, south to Florida and to Arizona and Mexico, and thus also has a greater range than its supposed model. The black female form of *P. glaucus* occurred as a small proportion of a population of predominantly yellow females found near Lake Placid in 1956. The distribution of frequencies of the black and yellow forms is not well known, but a predominance of black females seems to oc-

cur within the general range of abundance of the supposed model, *B. philenor.*

Local field collecting near the Archbold Biological Station provided adults of the species *P. troilus* and *P. glaucus,* while some *B. philenor* and *P. polyxenes* were captured as adults, and others were reared from eggs obtained from females in outdoor cages. The non-mimetic butterflies used throughout all the experiments as edible controls were collected locally as adults.

As in the earlier series of experiments, both male and female butterflies were used, and all were given to the birds in the manner described (Brower, 1958). In the case of *P. polyxenes,* although both sexes were given to each bird at some time, more females than males were used in the trials for the experimental birds. The three experimental birds were given *P. polyxenes* in the following proportions: 1 male, 5 females for E-1; 1 female for E-2; 1 male, 5 females for E-3. Each control bird was given 7 males and 3 females of *P. polyxenes.* Because all butterflies were offered on their sides with their wings folded dorsally, any sexually dimorphic color patterns of the upper wing surfaces were not visible to the birds, and only mimicry on the underside of the wings was being tested. The data indicated no difference in reaction to the butterflies by the birds based on the sex of any butterfly *per se.*

Procedure

In the present series, there were three experimental birds, E-1, E-2, and E-3, the same individuals used in the Monarch and Viceroy experiments. E-4, the experimental bird which failed to learn to reject unpalatable models on sight alone in the first series, was not included in this series. A replacement, E-4A, was given preliminary tests with various orders of insects, and trials with *B. philenor, P. troilus,* and non-mimetic butterflies during the course of these experiments. E-4A was thus accustomed to the procedure by the time the experiments in Part III were begun, but was not included in the present experiments.

E-1, E-2, and E-3 were given models (*B. philenor*) and non-mimetic butterflies (mostly *P. glaucus,* yellow females and males, but also *P. palamedes,* as noted above) successively in pairs; the order of presentation of each butterfly in any pair was determined with a table of random numbers. Each trial consisted of the presentation of 1 model and 1 non-mimetic butterfly to a bird. After from 30 to 50 trials, mimics (*P. troilus*) were substituted at intervals for the models. The method of substitution has been fully explained (Brower, 1958). The other two supposed mimics (*P. polyxenes* and *P. glaucus*) were substituted for the model by the same method, but only after a total of at least 70 trials per bird had been conducted in this series.

The procedure followed for the four control birds, the same individuals used in the earlier experiments, was altered in that the birds were given mimics only; the non-mimetic butterflies were omitted for the control birds in this experimental series. This change in procedure will be explained when the data are considered.

Results

The experimental birds:

Diagrams E-1, E-2, and E-3 (fig. 1, A & B) show the basic data for the reaction of the three experimental birds to non-mimetic butterflies, models, and mimics. All three diagrams indicate that without exception the non-mimetic butterflies (white circle) were eaten by all the experimental birds.

The diagram for E-1 shows that *B. philenor* (black circle) was killed (K), not touched (NT), or pecked (P) in the initial trials. At trial 16, E-1 ate one *B. philenor,* but following this no *B. philenor* was even touched throughout over 50 subsequent trials with that model. *P. troilus* (white square) was first offered to E-1 at trial 53, and was not touched.

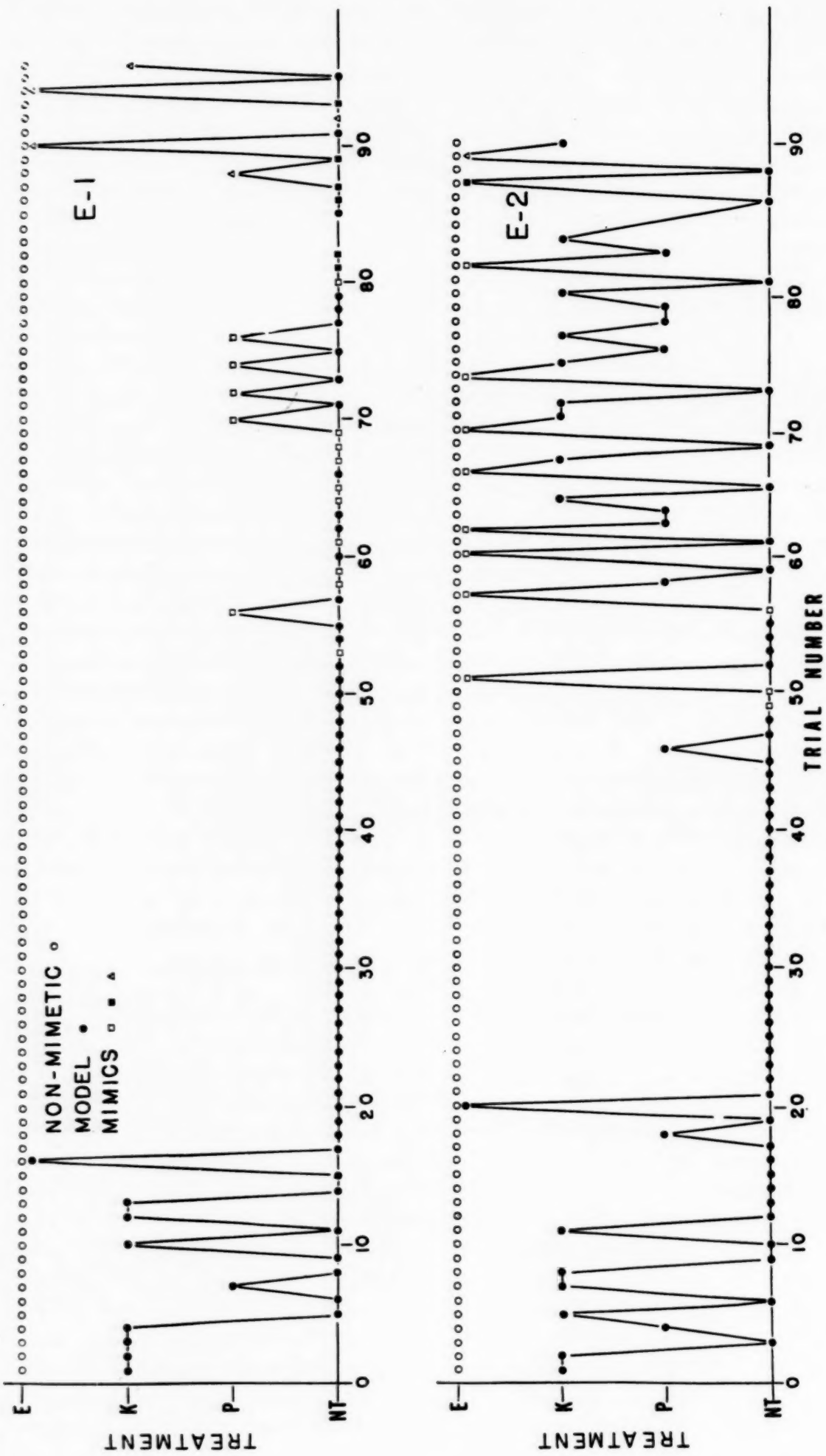

FIG. 1, A. Diagrams for experiments with *B. philenor* and *P. troilus*, *P. polyxenes*, and *P. glaucus*. Experimental birds E-1 and E-2.

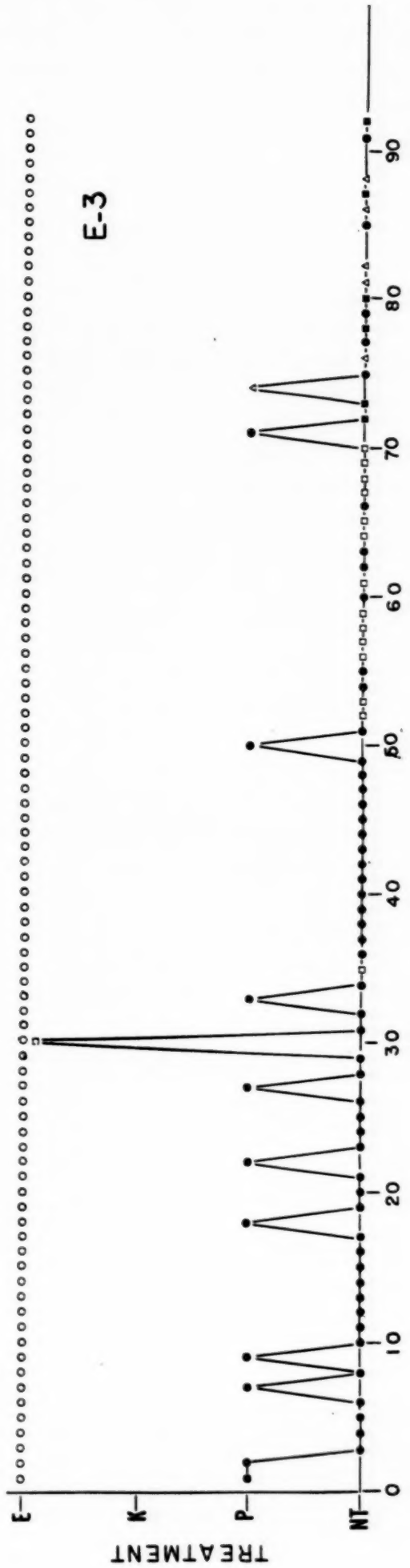

FIG. 1, B. Experimental bi[rd] E-3.

E-1 pecked *P. troilus* at trials 56, 70, 72, 74, and 76. However, *P. troilus* was not touched by E-1 in trial 80, and in nine intermittent trials between 56 and 70 inclusive (see fig. 1, A, diagram E-1). *P. polyxenes* (black square) was not touched in a total of six trials. However, *P. glaucus* (white triangle) was pecked, killed or eaten in four trials, and was not touched in only one trial.

The diagram for E-2 is initially like that for E-1. *B. philenor* was killed, not touched, or pecked until trial 20 when one *B. philenor* was eaten by E-2. Following this trial, E-2 did not touch *B. philenor* for 25 successive trials. When *P. troilus* was substituted for *B. philenor,* E-2 did not touch 2 *P. troilus*. However, as the trials progressed, E-2 ate *P. troilus* in most trials, and began to peck and kill *B. philenor* to a greater extent than in the initial trials (see fig. 1, A, diagram E-2). *P. polyxenes* and *P. glaucus,* substituted for the model in trials 88 and 90 respectively, were both eaten by E-2.

The diagram for E-3 shows that *B. philenor* was either pecked or not touched, but never killed or eaten by E-3. However, when *P. troilus* was substituted for the model at trial 30, it was eaten by E-3. A similar reaction was shown by this bird in the first substitution of a mimic for a model in the Monarch and Viceroy experiments in which E-3 killed the mimic (Brower, in press). In subsequent trials *P. troilus* was not touched. E-3 did not touch *P. polyxenes* in all six trials, but did peck the first *P. glaucus* at trial 74. All five *P. glaucus* which followed this trial were not touched.

A few general remarks may be made to recall the relationship between the two mimicry complexes studied thus far: I, the Monarch and Viceroy; and II, the *Battus philenor* complex. It should be remembered that the *B. philenor* experiments were commenced immediately after the Monarch and Viceroy experiments ended. Therefore the birds were already accustomed to the procedure when the *B. philenor* experiments began. The

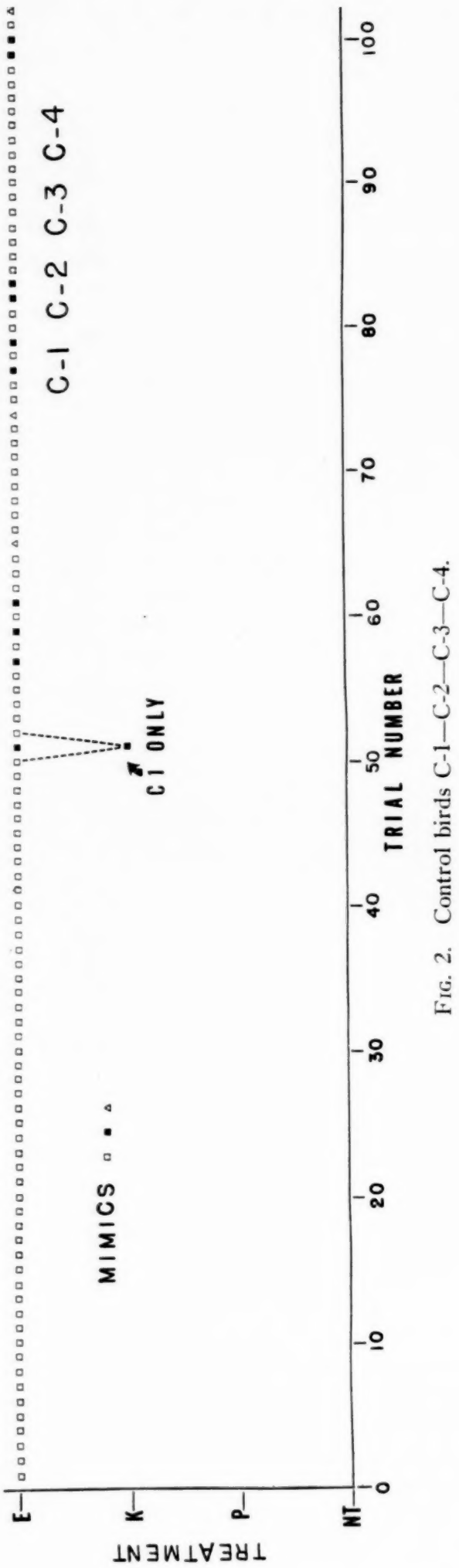

FIG. 2. Control birds C-1—C-2—C-3—C-4.

learning pattern was initially similar in both experiments, but two of the experimental birds appear to be reflecting their earlier experience with the Monarch in a general way in the *B. philenor* experiments. After the initial learning period, the diagrams for E-1 and E-2 show longer series of trials in which the model was not touched than were shown on the diagrams of the Monarch trials; there was a decrease in the number of "errors," i.e., when a model was "pecked" instead of "not touched" by a bird, from the first to the second series of experiments. This decrease in "errors" could mean that the memory of these birds was improving with experience, or possibly that *B. philenor* was more distasteful to them than the Monarch had been, and was not touched to a greater extent for that reason. The fact that E-1 and E-2 each actually ate one *B. philenor,* presumably a bad experience, might also have caused the longer series of trials for these birds in which the model was not touched.

During the present series of experiments the trials with the butterflies of the *B. philenor* complex were briefly interrupted in the case of the experimental birds. Two blank spaces can be seen on each of the diagrams for the experimental birds: for E-1, trial 83, 84; for E-2, trial 85, 86; for E-3, trial 83, 84. These spaces mark the memory tests that were given to each experimental bird in connection with the previous experiments with the Monarch and Viceroy. The results of these tests were mentioned in the earlier paper (Brower, 1958).

The control birds:

One diagram (C-1—C-2—C-3—C-4) (fig. 2) shows the basic data for the reactions to the mimics (*P. troilus, P. polyxenes,* and *P. glaucus*) by all four control birds. The responses to these mimics by the birds were identical with one exception: C-1 killed its first *P. polyxenes* at trial 51, whereas C-2, C-3, and C-4 ate their first *P. polyxenes* at trial 51 (see fig. 2, diagram C-1—C-2—C-3—C-4). In every other trial, of the 102 given to the birds, all mimics were eaten. Because of the uniform palatability of the mimics to all the control birds, the need for having non-mimetic butterflies to indicate the relative edibility of the mimics, compared to the known edibility of the non-mimetic butterflies, was eliminated. Furthermore, it was felt that the birds might have become satiated during 102 trials on a double ration of butterflies which they found palatable, i.e., the non-mimetic butterflies plus these palatable mimics. Therefore, as stated in the section on procedure, the non-mimetic butterflies were omitted from this experimental series in the case of the control birds.

Statistical Analysis of the Data

Table 1, A shows a comparison of the reaction to *P. troilus* by the experimental and control birds for the category "not touched" (NT) *vs.* "pecked—killed—eaten" (P–K–E). The two sets of birds clearly did not react to *P. troilus* in the same way (chi-squared = 301.96, d.f. = 6,P less than .001). The response differed significantly in so far as the control

Table 1. *Reactions of the experimental and control birds to* P. troilus

A. Comparison of no. "not touched" *vs.* no. "pecked–killed–eaten"

	Control birds				Experimental birds		
	C-1	C-2	C-3	C-4	E-1	E-2	E-3
NT	0	0	0	0	10	3	14
P–K–E	98	98	98	98	5	8	1

B. Comparison of no. "not touched–pecked–killed" *vs.* no. "eaten"

	Control birds				Experimental birds		
	C-1	C-2	C-3	C-4	E-1	E-2	E-3
NT–P–K	0	0	0	0	15	3	14
E	98	98	98	98	0	8	1

birds pecked, killed, or ate all the *P. troilus* presented to them, while the three experimental birds did not even touch *P. troilus* in 27 out of 41 trials (see table 1, A).

A comparison of the reaction to *P. troilus* by the two sets of birds for the categories "NT–P–K" *vs.* "E" was also made. The significant difference in response (chi-squared = 357.77, d.f. = 6, P less than .001) is shown on table 1, B: the control birds ate all the *P. troilus* presented to them, whereas the experimental birds ate only 9 out of 41 *P. troilus.*

Comparisons were also made of the reactions to *P. polyxenes* by the experimental and control birds (table 2). The significant difference in response in the first comparison (chi-squared = 38.76, d.f. = 6, P less than .001) can be attributed to the fact that the control birds pecked, killed, or ate all of the *P. polyxenes* presented, while the experimental birds did not even touch 12 out of 13; in the second comparison (chi-squared = 34.90, d.f. = 6, P less than .001) the control birds ate all but 1 *P. polyxenes,* whereas the experimental birds ate only 1 out of 13 *P. polyxenes.*

TABLE 2. *Reactions of the experimental and control birds to* P. polyxenes

A. Comparison of no. "not touched" *vs.* no. "pecked–killed–eaten"

	Control birds				Experimental birds		
	C-1	C-2	C-3	C-4	E-1	E-2	E-3
NT	0	0	0	0	6	0	6
P–K–E	10	10	10	10	0	1	0

B. Comparison of no. "not touched–pecked–killed" *vs.* no. "eaten"

	Control birds				Experimental birds		
	C-1	C-2	C-3	C-4	E-1	E-2	E-3
NT–P–K	1	0	0	0	6	0	6
E	9	10	10	10	0	1	0

TABLE 3. *Reactions of the experimental and control birds to the black female form of* P. glaucus

A. Comparison of no. "not touched" *vs.* no. "pecked–killed–eaten"

	Control birds				Experimental birds		
	C-1	C-2	C-3	C-4	E-1	E-2	E-3
NT	0	0	0	0	1	0	5
P–K–E	3	3	3	3	4	1	1

B. Comparison of no. "not touched–pecked–killed" *vs.* no. "eaten"

	Control birds				Experimental birds		
	C-1	C-2	C-3	C-4	E-1	E-2	E-3
NT–P–K	0	0	0	0	3	0	6
E	3	3	3	3	2	1	0

Table 3 gives comparisons of the reactions to *P. glaucus* by the experimental and control birds for the categories "NT" *vs.* "P–K–E" and "NT–P–K" *vs.* "E." As far as the limited data indicate, there was no significant difference in the responses to *P. glaucus* by the experimental and control birds (for A: chi-squared = 8.33, d.f. = 6, P less than .30, greater than .20; for B: chi-squared = 10.21, d.f. = 6, P less than .20, greater than .10). Further consideration will be given to a possible explanation of all of these results in the discussion.

In addition to the analysis of the responses to the butterflies by the birds, a tabulation was made of the mean reaction times of the birds in seizing models, mimics, and non-mimetic butterflies. The mean-time seize in seconds, the minimum-time-seize, the maximum-time-seize, the no. of each species seized, and the no. of each species "not touched" are shown for each bird (table 4). The table gives the mean time in seconds that each control bird took to seize *P. troilus* in the present series of experiments. It will be remembered that the non-mimetic butterflies were omitted. For the sake of com-

TABLE 4. *Reaction times of jays in seizing butterflies (in seconds to the nearest whole second)*

Birds	*B. philenor*					*P. troilus*					Non-mimetic butterflies				
	Mean time seize	Min. time	Max. time	No. seize	No. NT in 120"	Mean time seize	Min. time	Max. time	No. seize	No. NT in 120"	Mean time seize	Min. time	Max. time	No. seize	No. NT in 120"
C-1	—	—	—	—	—	1	1	5	98	0	3	1	14	92	0 *
C-2	—	—	—	—	—	4	1	15	98	0	5	2	25	95	0 *
C-3	—	—	—	—	—	1	1	2	98	0	1	1	3	101	0 *
C-4	—	—	—	—	—	5	1	34	98	0	6	1	76	94	0 *
E-1	6	2	25	10	59	7	2	24	5	10	2	1	6	96	0
E-2	15	2	59	28	50	4	1	10	8	3	1	1	2	90	0
E-3	36	4	120	10	52	3	3	3	1	14	3	1	17	92	0

* From Part I, Brower, 1958.

parison of the mean-time seize of the control birds for *P. troilus* and for non-mimetic butterflies, the mean-time-seize data for non-mimetic butterflies by the control birds in Part I (the Monarch and Viceroy experiments) (Brower, in press) are repeated here. It can be seen that the mean-time seize for *P. troilus* by each control bird is less than or the same as the mean-time seize for non-mimetic butterflies by the same birds. The implications of the reaction times of the control birds for *P. troilus* will be discussed later.

The mean-time-seize data for the three experimental birds for *B. philenor, P. troilus,* and the non-mimetic butterflies are also given. The mean-time seize for *P. troilus* in each case is less than or about the same as the mean-time seize for *B. philenor,* but is the same as or greater than that for the non-mimetic butterflies (table 4).

BEHAVIOR

In the first experimental series, with the Monarch and the Viceroy, the behavior of the experimental birds toward the unpalatable models was discussed (Brower, 1958). In the present experiments, the model *B. philenor* was also found to be unacceptable to the experimental birds. As before, the characteristic reaction of ruffling the feathers and shaking the body was given by each bird when the model or a mimic was placed in its cage. E-1 gave this reaction in 61 out of 69 trials (88%) with *B. philenor;* in 9 out of 15 trials (60%) with *P. troilus;* in 5 out of 6 trials (83%) with *P. polyxenes;* and in 2 out of 5 trials (40%) with *P. glaucus.* In the case of E-2, the ruffling reaction was given in 51 out of 78 trials (65%) for *B. philenor;* in 2 out of 11 trials (18%) with *P. troilus* (both of these being "not touched," see fig. 1, A, diagram E-2). E-2 did not give the feather-ruffling reaction for either *P. polyxenes* or for *P. glaucus,* both of which were eaten. The behavior of E-3 toward the model and mimics also included the feather-ruffling reaction in the following proportions of trials: in 24 out of 62 trials (39%) for *B. philenor;* in 2 out of 15 trials (13%) for *P. troilus* (those 2 being "not touched"); in 2 out of 6 trials (33%) for *P. polyxenes* (all 6 of which were "not touched"); and in 5 out of 6 trials (83%) for *P. glaucus.* For the experimental birds, the feather-ruffling reaction was limited to those trials in which the birds treated a butterfly as unacceptable, although the absence of the reaction did not guarantee the acceptance of a butterfly as edible.

The control birds did not show any ruffling of the feathers when they were given mimics, with one exception. C-3 in its first trial (51) with *P. polyxenes* did

give this reaction, although the bird ate the butterfly.

Discussion

The results of these experiments with *B. philenor* and its mimics *P. troilus, P. polyxenes,* and *P. glaucus* show that the experimental birds found the model *B. philenor* unpalatable. The three experimental birds showed rather different patterns of reaction to the mimics. E-1 never ate or killed *P. troilus.* However, in trials 70 to 76 (fig. 1, A, diagram for E-1) every *P. troilus* was pecked, while every *B. philenor* was not touched; this fluctuating sequence of trials would seem to indicate that E-1 was on the verge of regarding *P. troilus* as something different from *B. philenor.* It suggests that this bird was confused as to whether *P. troilus* is unpalatable like *B. philenor,* or is a different and edible species. In its confusion, E-1 never got beyond a superficial pecking of *P. troilus,* and apparently in these trials never found out that it is palatable. However, in the absence of the model, E-1 later did eat *P. troilus,* as discussed below. The present experiments with E-1 further showed that once the regular fluctuation of one *P. troilus* in a trial, followed by one *B. philenor* in the next trial, was broken by a series of three *B. philenor* trials, the bird no longer discriminated *P. troilus* from *B. philenor.* When *P. polyxenes* was given to E-1, it may be assumed that none was discriminated from *B. philenor,* because none was even touched by E-1. *P. glaucus* apparently was discriminated as something different from *B. philenor* and *P. polyxenes,* although in one trial *P. glaucus* was not touched, which shows that the bird was confused.

The discrimination by E-1 (and also by E-2 and in part by E-3) of *P. glaucus* from *B. philenor* is not surprising. In Florida, *P. glaucus* is especially large, and because of its size is sometimes considered a separate race, *P. glaucus australis* (Maynard). Furthermore, of the three mimics of *B. philenor* under consideration here, *P. glaucus* is the least like the model, particularly because its ground color is not a solid black, as it is in the other two mimics, but it has a lighter, brownish appearance, especially on the underside of the wings, which was the side offered to the birds. Finally, the Florida spring specimens of the model, *B. philenor,* which were used in these experiments were unusually small, so that the contrast between them and the large *P. glaucus* was greater than it might be later in the season, or in a region where the typical (smaller) *P. glaucus* is sympatric with the model. At this point it is well to remember that in experiments with caged predators, the predator has the opportunity for a closer, longer scrutiny of a butterfly than would usually be afforded in nature, where a bird might get only a glimpse of a flying butterfly. Thus the likelihood of a bird discriminating a mimic from its model is increased under laboratory conditions.

The reaction to the mimics of *B. philenor* by E-2 illustrates this last point. E-2 learned to "not touch" *B. philenor* on sight alone. After "not touching" two *P. troilus* (trials 49, 50), E-2 apparently discriminated the next *P. troilus* as something different from the model, and ate it. Thereafter, the fluctuations on the diagram for E-2 show that the bird had become quite confused. The following alternative interpretations seem possible: (1) E-2 found *P. troilus* palatable, and then temporarily mistook *B. philenor* for *P. troilus* immediately after each trial with *P. troilus.* Successive trials with *B. philenor* then reinforced the lesson of its unpalatability until a *B. philenor* again was not touched on sight alone. However, the next *P. troilus* offered in each case was eaten, and the bird's confusion as to the palatability of *B. philenor* reappeared. (2) After E-2 ate one *P. troilus,* it was then unable to discriminate *B. philenor* on sight alone from *P. troilus* with the result that almost all the models and mimics were seized indiscriminantly. This alternative assumes that E-2 seized

these butterflies by trial-and-error, and that in each case an unpalatable *B. philenor* was only pecked or killed, whereas a *P. troilus* was pecked, killed, found palatable, and then eaten. In either case, the bird was confused, and "mimicry" was working, although to the detriment of both model and mimic. The implications are that for this bird the numbers of *B. philenor* would have to be considerably greater than the numbers of *P. troilus* in an experiment of this kind for mimicry to work effectively. One *P. polyxenes* and one *P. glaucus* were given to E-2 just after the bird had not touched a *B. philenor* in each case; however, E-2 ate both of them.

Unlike E-1, which never fully discriminated *P. troilus* from *B. philenor,* and E-2, which ate *P. troilus,* E-3 apparently discriminated its first *P. troilus* from *B. philenor* and ate it, but did not even touch subsequent *P. troilus.* The fact that E-3 ate one *P. troilus* and did not touch later *P. troilus* seems difficult to interpret, in view of the palatability of this butterfly to E-2 and to the control birds. One can conclude either that E-3 found *P. troilus* unpalatable on the basis of one experience and therefore did not touch it again, or that E-3, after eating one *P. troilus,* was unable to discriminate those given in later trials from *B. philenor.* The latter conclusion seems the more likely for several reasons. First, the birds did not show the ability to learn absolutely the unpalatability of a butterfly species on the basis of one trial. It has been noted in the Monarch and Viceroy experiments, and also is evident in these experiments, that the birds showed intermittent "forgetfulness" of apparently learned unpalatability of model butterflies by pecking them at indefinite intervals throughout the trials. This pattern of "forgetfulness" can be seen on the diagram for E-3. At trial 30, the *P. troilus* was eaten; but at trial 33, the model *B. philenor* was pecked, and again at trials 50 and 71 *B. philenor* was pecked. However, between trials 50 and 71, 13 *P. troilus* and 7 *B. philenor* were not even touched on sight alone. This series of trials would seem to indicate that E-3 was not discriminating *P. troilus* from *B. philenor* as a different and palatable species.

Nevertheless, one would like to know why E-3 did eat the *P. troilus* at trial 30. It is possible that the mimic was given too early in the series in place of the model, and that the mimic fell on a trial when "forgetfulness" occurred and the bird would have pecked or killed any butterfly given. Once E-3 had killed *P. troilus* and found it palatable, the bird then ate the butterfly. It is also possible that E-3 did recognize the first *P. troilus* as something different from *B. philenor.*

E-3 did not even touch the *P. polyxenes* given, which indicates that this mimic was not discriminated from *B. philenor* or *P. troilus.* However, in the case of *P. glaucus,* E-3 apparently discriminated (pecked) the first *P. glaucus* given. Possible reasons for *P. glaucus* being readily discriminated from *B. philenor* by the experimental birds have already been discussed; these reasons also apply here. The subsequent *P. glaucus* given to E-3 were not even touched. In view of the fact that E-3 readily ate *P. glaucus* (yellow male and female) which was the nonmimetic butterfly used throughout these experiments, the rejection of the black female form of *P. glaucus* would seem to be associated with the bird's experience with the unpalatable black model. There is no reason to think that there is any difference in the palatability of the black and yellow forms of *P. glaucus,* on the basis of the uniform reactions to both color patterns by the control birds.

The data for the four control birds show that *P. troilus, P. polyxenes,* and *P. glaucus* are palatable. The results of the present experiments therefore do not agree with Poulton's (1909) hypothesis that the primary mimics of *B. philenor* are Müllerian and hence unpalatable to predators. Furthermore, Jones (1932), in outdoor feeding-tray experiments with passerine birds on Martha's Vineyard, noted that

P. troilus was edible to wild birds and rated it 100.0, highest in his system of relative edibility. In addition to the fact that the mimics were palatable, further substantiating evidence for their edibility is seen in the eagerness with which the control birds seized *P. troilus,* as shown by the mean reaction times on table 2.

Moreover, about one week after the commencement of trials in Part III (experiments to test mimicry in *Danaus gilippus berenice* (Cramer) and *Limenitis archippus floridensis* (Strecker), *P. troilus* was used in the position of a "non-mimetic butterfly," i.e., was given in couplet with *D. g. berenice* or *L. a. floridensis.* The palatability of *P. troilus* was substantiated with all eight birds in those experiments. The reaction to *P. troilus* by the experimental birds in the absence of the model *B. philenor* showed that E-1, E-2, and E-4A (replacement) each ate all of nine *P. troilus* offered. E-3 ate three out of five *P. troilus* given to it; however, E-3 did not touch the first *P. troilus* in those trials, which were given after an interval of nine days since this bird had had the last trial with *B. philenor* or its mimics. After about nine trials per bird with *P. troilus,* in which it was consistently eaten by three out of four experimental birds, one memory test was given to demonstrate the ability of the four birds to discriminate *B. philenor* from *P. troilus.* Each bird reacted to one trial with *B. philenor* as follows: E-1 and E-2 each killed one *B. philenor;* E-3 and E-4A each did not touch one *B. philenor.* Therefore two out of four experimental birds apparently could still reject the model on sight alone, after having learned that the mimic is edible.

The palatability of the mimics *P. troilus* and *P. polyxenes* has been shown and it is therefore concluded that under the conditions of the experiment, these butterflies are Batesian mimics of *B. philenor.* The problem is at once raised as to how mimicry could operate effectively in nature with two Batesian mimics (possibly three, if further, more extended experiments indicate that *P. glaucus* is also a mimic) living sympatrically with a single model. Very little is known about the relative numbers of models and mimics, but from my observations, *B. philenor* outnumbered the combined totals of *P. troilus, P. polyxenes,* and *P. glaucus* at least in one area in the Great Smoky Mountains of North Carolina in August, 1954. In other areas, for example south-central Florida, this is not the case.

Conclusions

The significant difference in response to the mimics *P. troilus* and *P. polyxenes* by the experimental and control birds is attributed to the fact that the former birds had experience with models, while the latter did not. The experimental birds learned that the model *B. philenor* was unpalatable and associated this unpalatability with its color pattern. When the mimics *P. troilus* and *P. polyxenes* were substituted for the model, two of the three experimental birds could not discriminate the color pattern of the mimics from that of the model. The third experimental bird apparently discriminated the mimics from the model, but then lost its ability to reject the model on sight alone, which indicates that mimicry was not working effectively. However, in spite of this bird, these experiments have shown that mimicry is effective in the case of *P. troilus* and *P. polyxenes,* under the conditions of the experiment.

There was no significant difference in the reaction to *P. glaucus* by the two sets of birds. This is in large part due to the fact that only small numbers of the black female form of that species were available for the experiments. The data do show that half of the *P. glaucus* offered were refused by the experimental birds on the basis of sight alone, whereas all the control birds ate every *P. glaucus.* The fact that the experimental birds refused any *P. glaucus,* in spite of the discrepancies between it and the model, suggests that there might be some selective advantage

for the mimicry of *B. philenor* by *P. glaucus*. However, the limited data available in these experiments have not demonstrated the effectiveness of mimicry in *P. glaucus*.

Summary

1) This paper is the second in a series of three which describe experimental studies of mimicry in some North American butterflies.

2) Seven caged Florida Scrub Jays (*Cyanocitta coerulescens coerulescens*) were used as predators in feeding experiments designed to test the effectiveness of mimicry in the butterflies *Battus philenor* (model) and the presumed mimics, *Papilio troilus, P. polyxenes,* and the black female form of *P. glaucus*. The butterflies were immobilized and their wings were folded together dorsally, so that only mimicry in the characters of the underside of the wings was being tested.

3) The three experimental birds ate all the non-mimetic butterflies, which were offered in couplet with each model or mimic presented. Because the mimics proved to be completely palatable to the control birds, these birds were not offered the edible, non-mimetic butterflies in the present experiments.

4) The model *B. philenor* was unpalatable to all three experimental birds.

5) After successive trials with the model, the mimic, *P. troilus,* was offered to the experimental birds in place of the model. Two of the three experimental birds did not discriminate *P. troilus* from *B. philenor*. The third experimental bird ate *P. troilus*. However, this bird then lost its ability to reject *B. philenor* on sight alone, which indicated that discrimination by sight was not effective between the mimic and model.

6) When *P. polyxenes* was given, it was not discriminated from the model, *B. philenor,* by the same two experimental birds which had failed to recognize *P. troilus* as different from *B. philenor*. The third experimental bird apparently did discriminate *P. polyxenes* from *B. philenor*.

7) When the black female form of *P. glaucus* was given in place of the model, it was apparently discriminated by two of the three experimental birds. The third bird, in this case, did not discriminate *P. glaucus* from *B. philenor*.

8) The same characteristic behavior that had been shown by the experimental birds toward the Monarch and the Viceroy was again evident when *B. philenor* and its mimics were presented.

9) The four control birds, which never were given the model, found *P. troilus, P. polyxenes,* and the black female form of *P. glaucus* palatable; the mean time which each control bird took to seize *P. troilus* also indicated that it was particularly palatable.

10) A comparison of the reaction of the experimental and control birds to *P. troilus,* and a comparison of their reaction to *P. polyxenes,* both gave values for P of less than .001. The significant difference in response in each case is attributed to the fact that the experimental birds had experience with models before receiving the mimics. The unpalatability of *B. philenor* was associated with its color pattern; the birds then could not discriminate or confused the color pattern of the mimics with that of the model. Under the conditions of the experiment, the effectiveness of mimicry in *P. troilus* and *P. polyxenes* has been demonstrated, and both have been shown to be Batesian mimics.

11) A comparison of the reaction of the experimental and control birds to the black female form of *P. glaucus,* on the basis of a small number of trials, showed no significant difference between the two sets of birds in their treatment of this butterfly, but the possibility of the mimicry of *B. philenor* by *P. glaucus* was clearly suggested by the experiments. Explanations of the discrimination of *P. glaucus* from *B. philenor* by two of the three experimental birds have been given.

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CYTOTAXONOMIC STUDIES ON THE FERN GENUS *PELLAEA*

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INTRODUCTION

Apogamy in ferns involving the premeiotic doubling of the chromosome number has recently been reported by Manton (1950) to occur in several unrelated species including *Pellaea atropurpurea*. A second report was made of apogamy in *Pellaea*, in a floristic survey of the chromosome numbers of ferns of eastern North America, by Britton (1953) in *P. glabella* var. *glabella*. The present investigation was undertaken as a cytological survey of a group of closely related species with particular reference to apogamy, when it was noted in a revision of *Pellaea* section *Pellaea* Tryon (1957) that the relationships of several entities in the group were complicated by apogamy and apparently hybridization. The genus *Pellaea* belongs to the tribe *Cheilantheae* of the *Polypodiaceae* and the fifteen species included in section *Pellaea* are predominately Cordilleran, growing in dry, rocky habitats, under semi-desert conditions quite unlike that usually associated with ferns.

APOGAMY

In order to understand apogamy in *Pellaea*, it is necessary to be familiar with the phenomenon in other ferns (Manton, 1950, pp. 158–170). Four patterns of sporangial development that occur in apogamous ferns are described. These patterns which may occur in the same plant, or even in the same sorus, may be characterized by the number of spore mother cells in the sporangium as follows:

1. Sporangia with sixteen spore mother cells.
2. Sporangia with eight spore mother cells.
3. Variant of (2) with incomplete and irregular cleavage.
4. Sporangia with four giant spore mother cells.

After meiosis the 16 spore mother cells of the first type produce 64 spores per sporangium which usually abort. The sporangia of the second type produce 32 mature spores per sporangium which are usually monolete and larger than those of the 64-spored type. Only 16 giant spores are found in a mature sporangium of the fourth type.

In apogamous ferns there is no haploid stage and the chromosome number is the same in both the gametophyte and the sporophyte. A compensating mechanism for the absence of fertilization occurs in the second pattern where there is a premeiotic doubling of the chromosomes, which gives the spore mother cells a temporary constitution of $4n$ before meiosis. Subsequently, the number of bivalents present at diakinesis in a spore mother cell from a sporangium with eight spore mother cells, determines the $2n$ or sporophytic chromosome number. This raises a reporting difficulty which Manton (1950) overcomes by referring to the "n" of apogamous ferns. If this is done, then "n" and $2n$ are numerically equal.

The number of bivalents at diakinesis in a spore mother cell from a sporangium with four spore mother cells (pattern 4), is double the sporophytic chromosome number, or the $4n$ number, because there are two premeiotic chromosome doublings in this pattern of development.

It should be noted that the greatest interest is attached to observations of meiosis in the spore mother cells of the sixteen celled sporangia (pattern 1), because

in these, there has been no premeiotic doubling of the chromosomes, and the pairing relationships of the chromosomes will represent their true homologies, rather than the pairing of duplicated chromosomes.

Normal sexual species of Pellaea, in contrast to the above patterns, have mature sporangia with 64 smaller, usually trilete spores. Accordingly, it is possible to examine the sporangia and if 32 spores are found, it may be assumed that the specimen is apogamous. Such types may then be geographically plotted from herbarium specimens.

Apogamy also affects the gametophytic phase of ferns. One or both sex organs may be suppressed. In *Pellaea* it was observed that spores from the 32 spored sporangium produced prothallia bearing only antheridia but embryos were subsequently formed. Dr. Lenette Rogers Atkinson (Amherst, Massachusetts) who specializes in studies of fern gametophytes, expressed an interest in this matter, and material of both sexual and apogamous species were sent to her for study. In addition to confirming our observations on the absence of archegonia on the prothallia of apogamous types, Dr. Atkinson made the following observations which are of interest here. "In agar cultures grown under the most favorable conditions of lighting, neither archegonia nor antheridia were observed in *P. glabella* var. *glabella* although embryos were formed. In similarly grown cultures of *P. atropurpurea, P. sagittata* var. *sagittata,* and *P. ovata,* all having 32-spored sporangia, archegonia were not observed but occasionally antheridia appeared on the posterior part of the thallus or on small thalli growing among the rhizoids of the larger ones. In *P. sagittata* var. *sagittata* a few empty antheridia were observed. Hairs or scales surrounding the embryos at the notch of the prothallus were observed in all of these apogamous species. In the cultures of the apogamous prothallia it was observed that all of the plants produced embryos at the same time." Since antheridia are formed on apogamous prothallia, the possibility exists that they may produce functional male gametes. Such crosses have been made by Döpp (1939) in the synthesis of hybrids using the antheridia of an apogamous strain of *Dryopteris Borreri* and the archegonia of *D. Filix-mas,* and indicate that the apogamous forms are still able to function as male parents, even if their usual mode of reproduction is without feritilization. Figure 2, prepared by Dr. Atkinson, illustrates early stages of embryo development in apogamous prothallia.

Materials and Methods

Most of the specimens were collected by the senior author. We are indebted to W. J. Thompson for collections of *P. glabella* var. *simplex* which is of rare and local occurrence in Washington and to Dr. Seville Flowers for collections of *P. Breweri* and Dr. and Mrs. G. B. Ownbey who supplied us with abundant material of *P. glabella* var. *occidentalis.* Young fronds were fixed in a solution of three parts of absolute alcohol to one part of glacial acetic acid and were shipped to the junior author for cytological examination. The cytological methods used by Britton (1953) were employed without modification. Voucher specimens have been deposited in the herbarium of the Missouri Botanical Garden.

Observations

The chromosome number determinations and the entities studied are given in table 1. The taxonomic nomenclature is that of Tryon (1957).

Of particular interest are the five sexually reproducing diploids that were found in the genus, because each is a potential progenitor on cytogenetic grounds of the triploids and tetraploids.

The occurrence of a sexually reproducing tetraploid form of *P. ternifolia* var. *ternifolia* is also noteworthy, because the other tetraploids studied in the genus are apogamous. Meiosis was quite regu-

TABLE 1. *Chromosome numbers of* Pellaea

Species	Locality and Collection	Mode of reproduction	Meiotic chromosome numbers[a]	Ploidy
P. glabella Mett. ex Kuhn var. *occidentalis* (E. Nelson) Butters	Laramie Hills, Wyo. *G. B. & F. Ownbey 1676*	Sexual	29	2X
var. *glabella*	Rattlesnake Point, Ontario[b]	Apogamous	116	4X
var. *simplex* Butters	Columbia River, Wash. *J. W. Thompson 17246*	Apogamous	116	4X
P. Breweri D. C. Eaton	Wasatch Mts., Utah *S. Flowers* on July 25, 1953	Sexual	29	2X
P. atropurpurea (L.) Link	Gray Summit, Mo. *R. M. & A. F. Tryon 5523*	Apogamous	87	3X
P. ternifolia (Cav.) Link var. *ternifolia*	Cuernavaca, Mexico *R. M. & A. F. Tryon 5105*	Sexual	29	2X
	Valle de Bravo, Mexico *R. M. & A. F. Tryon 5141*	Sexual	58	4X
var. *Wrightiana* (Hook.) A. F. Tryon	Inks Lake, Texas *R. M. & A. F. Tryon 5161*	Sexual	—	—
P. sagittata (Cav.) Link var. *cordata* (Cav.) A. F. Tryon	Real del Monte, Mexico *R. M. & A. F. Tryon 5124*	Sexual	29	2X
	University City, Mexico *R. M. & A. F. Tryon 5147*	Sexual	29	2X
var. *sagittata*	Cuernavaca, Mexico *R. M. & A. F. Tryon 5103*	Apogamous	87	3X
	Morelia, Mexico *R. M. & A. F. Tryon 5153*	Apogamous	87	3X
P. ovata (Desv.) Weatherby	Marble Falls, Texas *R. M. & A. F. Tryon 5524*	Sexual	29	2X
	Valle de Bravo, Mexico *R. M. & A. F. Tryon 5134*	Apogamous	—	—

[a] For those forms which are apogamous, the number of chromosomes is that observed in spore mother cells from sporangia of eight spore mother cells.

[b] Britton (1953).

lar in this form and apparently only bivalents are formed (fig. 1, B).

It was hoped that some sporangia with sixteen spore mother cells in *P. glabella* var. *simplex* could be found. An extended and extensive search failed to reveal any, however, and it was considered that if they do occur, they do so infrequently. A few such spore mother cells were seen in *P. glabella* var. *glabella*. In these, there were approximately 20 univalents and the remainder were bivalents or multivalents. The picture there was never clear enough to present a definitive analysis of the pairing relations of the chromosomes. The tentative suggestion is that one genome is not homologous with the other three.

The two triploids, *P. atropurpurea* and *P. sagittata* var. *sagittata* both presented a similar cytological picture. Observations on spore mother cells from the sporangia with sixteen spore mother cells indicated that there were 20–29 univalents and approximately 29 bivalents per cell. These observations on *P. atropurpurea* are similar to those of Manton (1950, pp. 184–185).

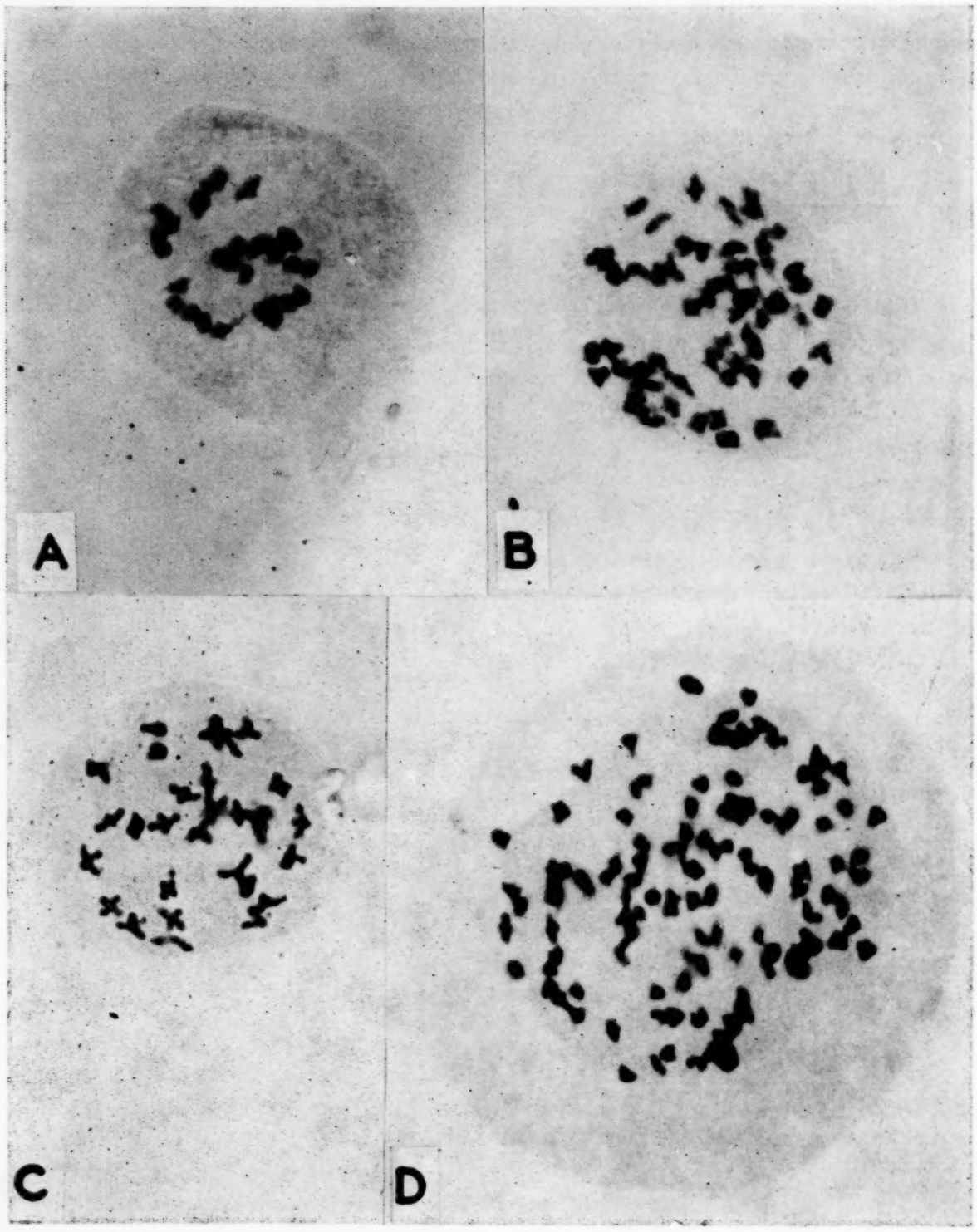

FIG. 1. A. Metaphase I in spore mother cell of *P. ternifolia* var. *ternifolia* ($n = 29$). B. Diakinesis in spore mother cell of *P. ternifolia* var. *ternifolia* ($n = 58$). C. Diakinesis in spore mother cell of *P. ovata* from sporangium of 16 spore mother cells ($n = 29$). D. Late diakinesis in spore mother cell of *P. glabella* var. *simplex* from sporangium of 8 spore mother cells ("n" $= 2n = 116$). Magnification 1,000 ×.

Pellaea sagittata var. *sagittata* was the only species in which sporangia with four giant spore mother cells were seen. There is a possibility that these later abort because all the mature sporangia examined had 32 spores. None were seen with 16 mature spores.

The 29 chromosomes at metaphase I from *P. ternifolia* var. *ternifolia* are shown in figure 1, A, while the 58 chromosomes from the tetraploid form of the same species are shown in figure 1, B. A spore mother cell from *P. ovata* with $n = 29$ is shown in figure 1, C. Figure 1, D shows a spore mother cell of *P. glabella* var. *simplex* which may be considered repre-

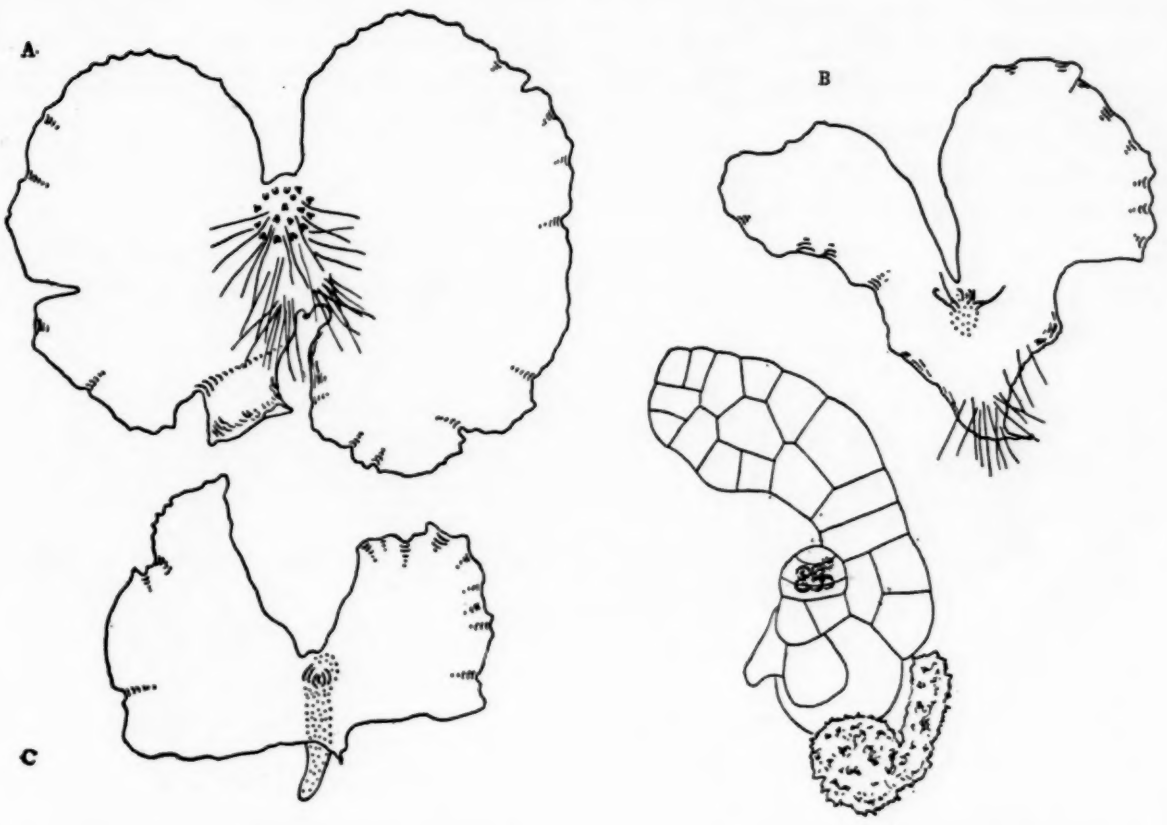

FIG. 2. Gametophytes. A. *P. glabella* var. *occidentalis,* ventral surface with rhizoids and several archegonia with open necks. × 12. B. *P. glabella* var. *glabella,* central surface, apogamous embryo stippled and with scales. × 12. C. *P. atropurpurea,* (left) dorsal surface, apogamous embryo stippled and with scales. × 12; (right) small thallus bearing antheridium with antherzoids. × 180.

sentative of the chromosomes of an apogamous tetraploid. In general morphology, the chromosomes of the species of *Pellaea* are similar to one another. This is not apparent from the photographs because of the different stages represented, but is quite evident after one has studied different species over an extended period of time.

DISCUSSION

The highest polyploids "*n*" and $2n = 116$ are found in *P. glabella* which also has more intraspecific entities than other species in the section. In this complex, the tetraploid varieties—*glabella* in the eastern United States and *simplex* in the west—are distinguished from the diploid var. *occidentalis* by the larger, generally more divided leaves. The tetraploid varieties are apogamous and have sporangia bearing 32 spores in contrast to the smaller leaved diploid which occurs in the Black Hills of South Dakota, northward to Alberta, Canada, with 64 spores per sporangium, normal sexual prothallia and a monoploid chromosome complement of 29 (fig. 3). Thus var. *occidentalis* appears to be the source, at least in part, of the tetraploids.

The origin of the triploids *P. atropurpurea* and *P. sagittata* var. *sagittata* is uncertain, although the possibilities from the cytological evidence are more definite. Triploidy is discussed by Manton (1950) in the cases of *Dryopteris Borreri, D. atrata* and *Pteris cretica* on the logical grounds that a triploid would necessarily originate from two different ancestors. *P. atropurpurea,* a conspicuous member of the fern flora of the eastern United States, is considered by Manton, on the basis of the equal number of pairs and univalents, to be a backcross between an allotetraploid and one of its diploid parents, pending the existence of a member

FIG. 3. Distribution of *Pellaea glabella* with plant and pinna, var. *occidentalis* center; var. *glabella*, right; var. *simplex*, left.

having a monoploid complement of 29. Several species in the section are now reported with this chromosome number.

The origin of the second triploid, *P. sagittata* var. *sagittata* which occurs in Mexico southward to Bolivia (fig. 4) likewise can be explained as a hybrid between a tetraploid and a diploid. Variety *sagittata* is apogamous and 15–29 univalents have been observed at metaphase I of meiosis. One genome appears to have been received from the closely allied diploid, *P. sagittata* var. *cordata* which occurs in southern Texas and Mexico. The characteristics by which var. *sagittata* can be distinguished from var. *cordata*—the sagittate form of the segments, the pubescence, and the flexuous rachises—are essentially those which characterize the other parental possibility—*P. ovata*. This latter species occurs in Texas southward to Argentina and there is a widely distributed apogamous strain occurring in some localities with *P. sagittata* var. *cordata* which may have crossed with var. *cordata* to produce the var. *sagittata*.

The diploids in the section appear to be as abundant as the polyploids, for of the nine entities which have been cytologically examined, five—*P. Breweri, P. glabella* var. *occidentalis, P. ternifolia* var. *ternifolia, P. sagittata* var. *cordata* and *P. ovata*—have the haploid number of 29. These are of special interest for it has already been noted that the polyploid forms are most likely derived from them. Among the diploids *P. Breweri* and *P. glabella* var. *occidentalis* morphologically are allied closely and in several characters the two resemble some species of *Cheilanthes* which occur within the same general geographic range. In *P. ternifolia* var. *ternifolia,* it was observed that a tetraploid form occurs in central Mexico. The absence of any multivalent pairing in this form, indicated that it may be an allopolyploid or possibly an ancient autopolyploid. The morphological resemblance of the tetraploid to the diploid plants would support the latter supposition.

Further studies are desirable in the closely allied species *P. intermedia* and *P. andromedaefolia*. Both have 32- and 64-

spored races which suggests that some plants are apogamous and polyploid and some are sexual and diploid. In the apogamous plants, some sporangia may be found in which 16 spore mother cells are formed, but in these, the spores usually abort. However, in *P. intermedia* there may be an exception to this condition, for two specimens from the Chisos mountains in Texas have leaves bearing both 64- and 32-spored sporangia. This may represent an apogamous type in which both eight and sixteen spore mother cells are formed, but in which the products of the sixteen spore mother cells do not abort.

The occurrence of apogamy in such un-

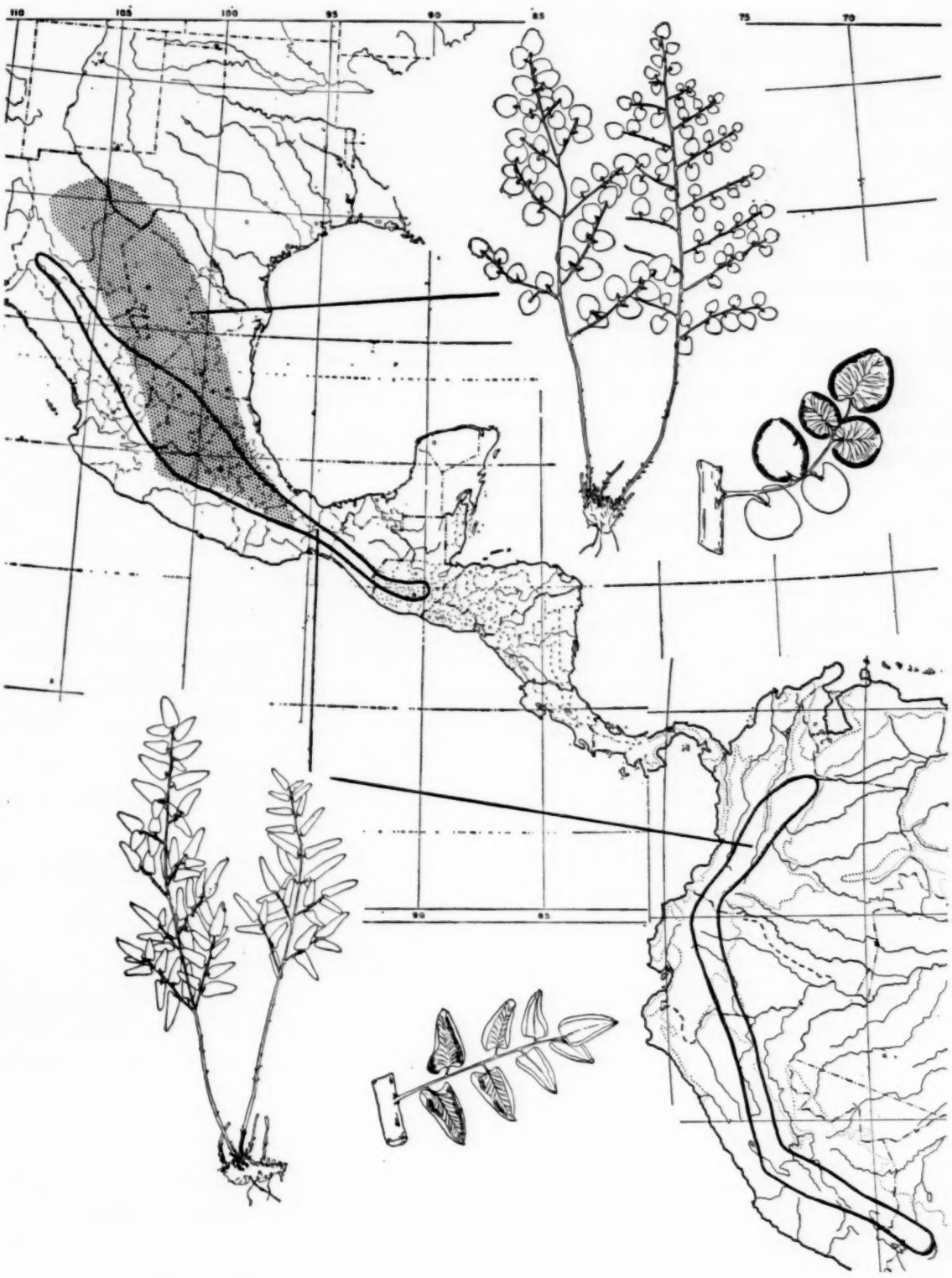

FIG. 4. Distribution of *Pellaea sagittata* with plant and pinna, var. *cordata,* above; var. *sagittata,* below.

related genera as *Pteris, Asplenium, Dryopteris* and *Pellaea* indicates that the mechanism may have had independent origins in several genera. In *Pellaea* the apogamous entities which have been observed are polyploids—two tetraploids and two triploids. These last are almost certainly of hybrid origin. The apogamous types in *P. sagittata* and *P. ovata* are evidently closely related and the mechanism may have been inherited by *P. sagittata* var. *sagittata* from *P. ovata.* However, apogamy also occurs in *P. glabella* and *P. atropurpurea* which are only distantly related to the former species and, in *P. glabella,* the possibility exists that the mechanism may have arisen independently of hybridization, for there are both sexual and apogamous races.

Some information is available from the geographic data on the probable migration of the species. It is logical to assume that the apogamous members would have an advantage over the normal sexual types in that they would not require the moisture necessary for fertilization. This presumably would be a critical factor here, for these ferns generally occupy dry, rocky habitats. The region in which the sexual ancestors exist may be regarded as a center of differentiation. With the exception of *P. Breweri* and *P. glabella,* all members of the section either occur in the southwestern United States and adjacent Mexico, or they seem to be derivatives of those that do. In *P. glabella* the apogamous varieties extend the range from an area around the northern Rocky mountains eastward to Tennessee and Vermont and westward to Washington and Arizona. It is significant that most of the species with ranges extending into the Andes are apogamous, and it seems likely that they have migrated southward from the area of the sexual types in Mexico. If the direction of migration is thus established, it might be extrapolated to species in *Notholaena* and *Cheilanthes* occurring in similar habitats and having comparable ranges.

Summary

The basic chromosome number of 29 has been established for the fern genus *Pellaea* section *Pellaea* on the basis of five sexually reproducing diploids. In addition, two apogamous triploids, two apogamous tetraploids and one sexually reproducing tetraploid have been observed in this group.

The normal sexual plants have sporangia bearing 64 small, mostly trilete spores and the apogamous types have 32 larger, mostly monolete spores. Thus it is possible to distinguish the two types in herbarium specimens and to plot their geographic ranges.

In the apogamous examples studied, the gametophytic stage has one or both sex organs suppressed although embryos are formed.

Apogamy appears to be related to hybridization, particularly in the triploid entities *P. sagittata* var. *sagittata* and *P. atropurpurea.* In *P. glabella* both sexual-diploid and apogamous-tetraploid types have been observed and there is less certainty of a hybrid origin in the latter.

Migration into South America from the Southwestern United States and Mexico is indicated by the relative distribution of the sexual and apogamous types in *P. sagittata* and *P. ovata.*

Acknowledgments

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A DIFFERENTIATION INDEX, AND A NEW MEASURE OF EVOLUTIONARY RATES

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INTRODUCTION

Paleontological studies of relative growth have shown that allometric growth pattern may often remain stable during long evolutionary sequences; but also that clear-cut shifts from one growth pattern to another may occur. As examples may be noted the results of Robb (1935), later developed in more detail by Reeve and Murray (1942); Phleger and Putnam (1942); Kurtén (1954 a, b). Most of these studies concerned only one or a few variate pairs. However, it may be useful to extend the method to a greater number of variate pairs. It is then possible to study the relative frequency of identical and differentiated growth patterns in the populations compared; and this may be expressed as an "index of differentiation," giving the percentage of significantly differing allometry trends.

This index may be expected to run more or less parallel with actual taxonomic and genetic differentiation, because the growth patterns have a genetic basis, and changes in them arise from genetic change. It is suggested that this index may be used as a taxonomic character, to help us infer whether the populations we are comparing belong to one species or two, to two subspecies or only two slightly differentiated demes not meriting formal recognition. I do not mean that it should be the sole basis for such conclusions, but it may contribute in a valuable way; it should give highly objective characters, which may be useful as a guide in decisions on border-line cases in taxonomy.

In order to make the method serviceable, the first step is to compare populations in which the taxonomic relationships are already well known. Indices obtained by such studies will indicate the scale of differentiation which we may expect on the deme, subspecies, and species level, and so on.

Being quantitative, the method will also yield a measure of evolutionary rates. If the lapse of time between ancestral and descendant population is known, we have an absolute measure; but it may also be used as a relative measure, when two collaterally evolving phyla are studied at an earlier and a later point in time.

In view of these interesting potentialities, some examples are given in the present paper. The main object of study has been the Pleistocene to Recent evolutionary series of the spotted hyena; but I have also drawn on hitherto unpublished data assembled by myself and Dr. Robert Rausch (Anchorage, Alaska) in joint studies of Recent circumpolar species; and on selected published data.

EVOLUTION OF THE SPOTTED HYENA

The evolution of the spotted hyena was discussed in Kurtén (1956). Numerous measurements of teeth and other skeletal parts were taken and subjected to allometry analysis, the different samples being compared by means of analysis of variance. Details on the treatment will be given elsewhere.

The following populations were studied (data on the samples in Kurtén, 1956); the ages are taken from Zeuner (1946), a dating which is much disputed, though probably on the right order of magnitude.

Crocuta c. crocuta, the Recent spotted hyena, Africa.

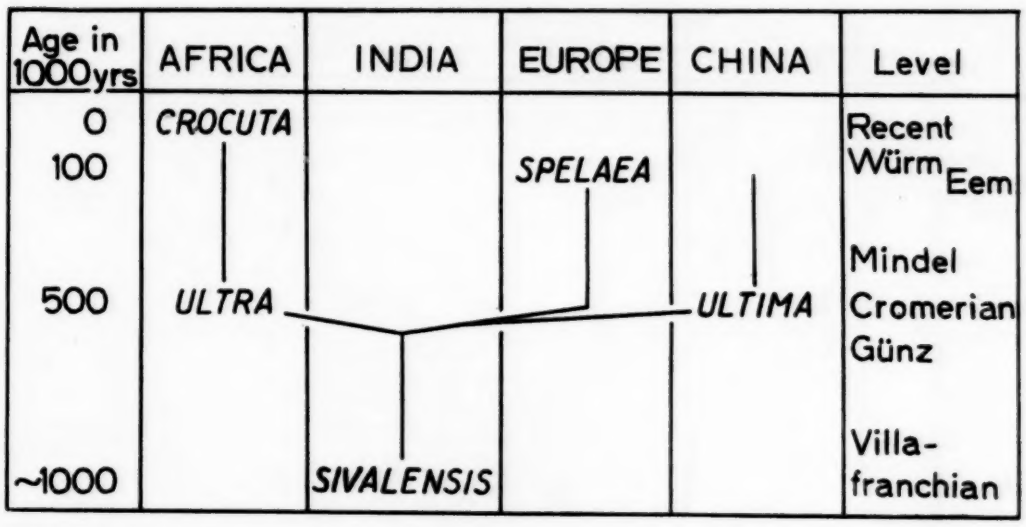

FIG. 1. Evolutionary, temporal and geographic relationships of the populations (*Crocuta sivalensis* and four subspecies of *C. crocuta*) discussed in this paper.

Crocuta c. spelaea, the cave hyena, late Pleistocene, Europe. Age from 100,000 years to perhaps 20,000 years.

Crocuta c. ultima, middle Pleistocene (Cromerian), China. Approximate age 500,000 years.

Crocuta c. ultra, middle Pleistocene (Cromerian), South Africa. Approximate age 500,000 years.

Crocuta sivalensis, early Pleistocene (Villafranchian), India. The age is very uncertain, probably at least 800,000 years if the other estimates are correct. It may be substantially more, though probably not in excess of twice that figure; one million years is here taken as an approximation.

The probable evolutionary relationships between these populations are indicated in figure 1. *Crocuta sivalensis* is the ancestral species. By Cromerian time, it had evolved into *C. crocuta,* which rapidly spread into the Palearctic and Ethiopian regions, differentiating into local subspecies. The early South African immigrant *C. c. ultra* apparently partakes in the ancestry of the living population. The Chinese *C. c. ultima* persisted to the late Pleistocene, but only middle Pleistocene specimens have been available to me. In Europe the immigration of the species is recorded in the Cromerian, but samples of that age are too small (or inadequately published) to give useful information on allometry trends; late Pleistocene material is plentiful.

The samples of the living subspecies and of the late Pleistocene cave hyena (*spelaea*) are fairly large, the other three are small; the examples given below indicate the size of the samples.

ALLOMETRY DIFFERENTIATION

The method may be illustrated by a comparison of the growth patterns of width and length in the third lower premolar, P_3, in the various populations. Table 1 gives the statistics, and in figure 2 the observation pairs are plotted on a logarithmic scatter diagram. Means and trend lines are given for all five samples.

TABLE 1. *Allometry parameters for one sample of* Crocuta sivalensis *and four samples of* C. crocuta, *P_3 width on length*

Sample	N*	$M_{\log W}$	$M_{\log L}$	k
Crocuta sivalensis	5	1.154	1.292	0.97
C. c. crocuta	43	1.154	1.306	1.12
C. c. spelaea	142	1.220	1.357	1.14
C. c. ultima	6	1.243	1.368	0.84
C. c. ultra	7	1.134	1.314	0.90

* N, size of sample; M, mean; k, coefficient of allometry.

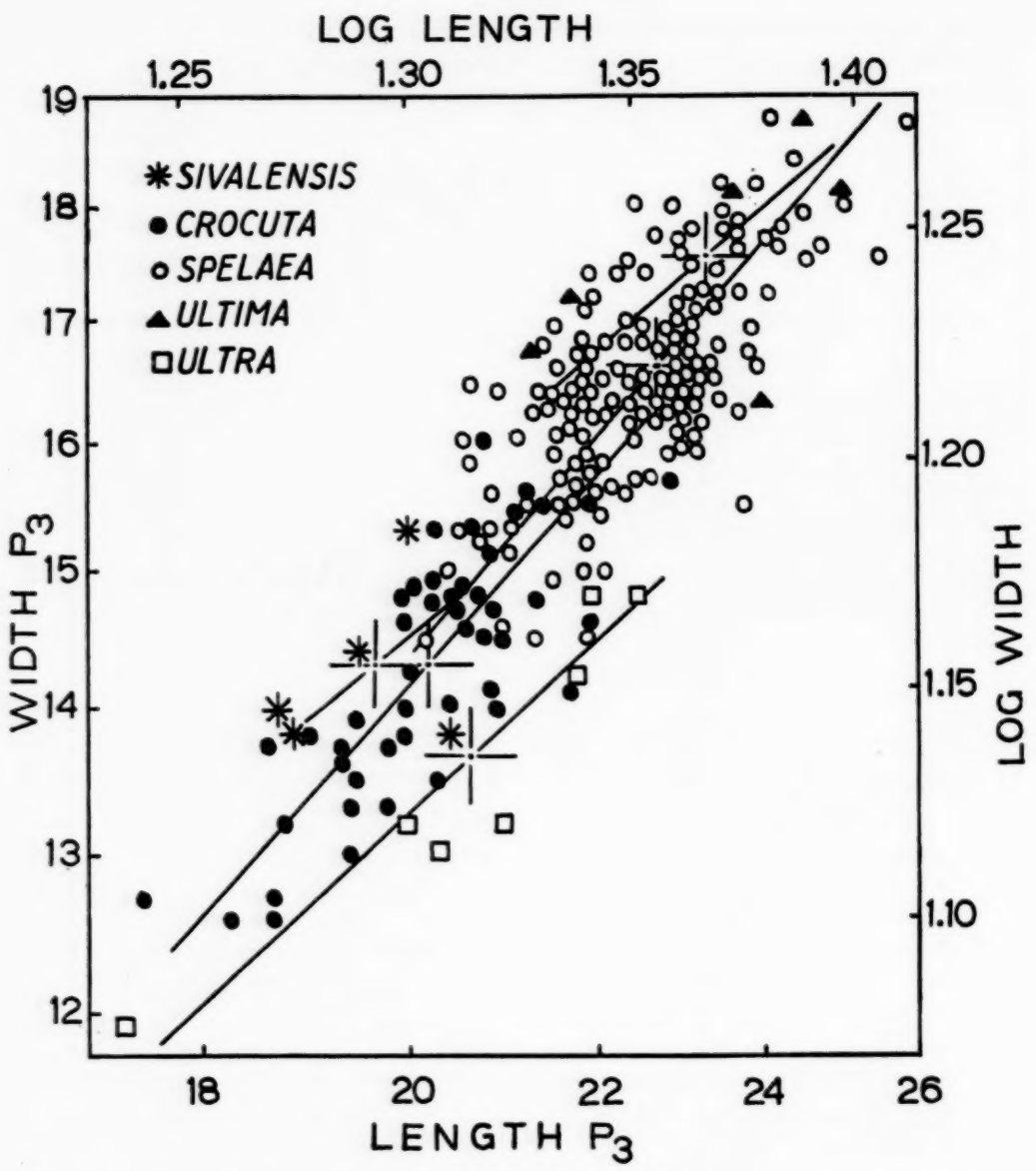

FIG. 2. Covariation of width and length of third lower premolar in the *Crocuta* samples, with means and trend line for each.

Tests for significance were made between all samples. The results are shown in table 2, and it is seen that all differences are significant or probably significant, except that between the growth patterns of *C. sivalensis* and *C. c. crocuta*. It may thus be concluded that all subspecies of *C. crocuta* are differentiated in regard to this growth pattern, but that the living *C. c. crocuta* may still retain the ancestral pattern of *C. sivalensis*.

TABLE 2. *Significance of differences in regressions width/length P_3 between samples of table 1*

Comparison	N_1+N_2	F*	P
sivalensis—crocuta	48	3.18	>0.05
sivalensis—spelaea	147	37.5	<0.001
sivalensis—ultima	11	29.0	<0.001
sivalensis—ultra	12	8.0	<0.02
crocuta—spelaea	185	33.9	<0.001
crocuta—ultima	49	17.3	<0.001
crocuta—ultra	50	17.8	<0.001
spelaea—ultima	148	6.14	~0.02
spelaea—ultra	149	56.1	<0.001
ultima—ultra	13	31.8	<0.001

* F, variance ratio; P, probability value.

As another example may be taken the covariation between length of palate and (basal) length of skull. This relationship (fig. 3) is is not known for *C. c. ultra*, but for the other samples the analysis failed to reveal any significant differences, and it is concluded that the character was inherited without change from *C. sivalensis* to the three subspecies *crocuta, spelaea* and *ultima*.

Twenty-four different allometry relationships were studied in the same way, in

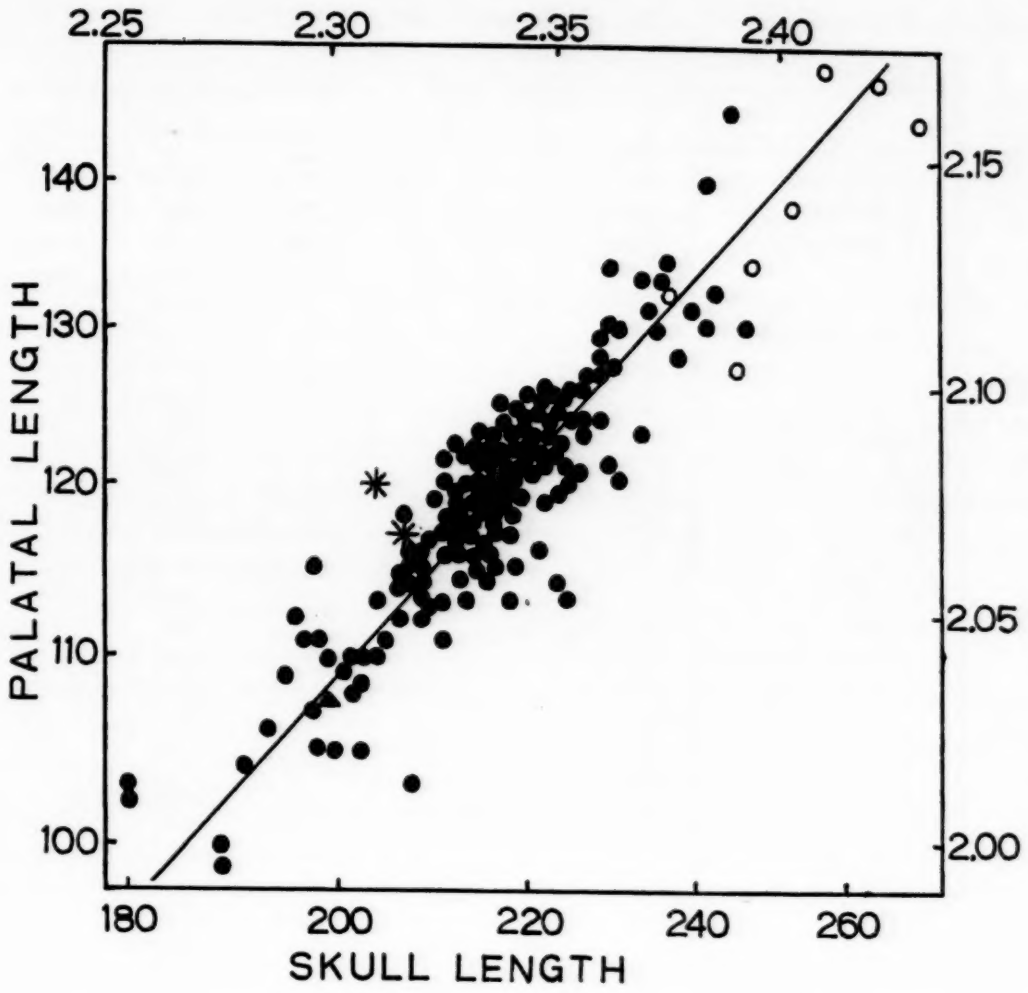

FIG. 3. Covariation of palatal length and skull (prosthion-basion) length. Symbols and log scales as in figure 2.

C. c. crocuta and *C. c. spelaea;* only a part of them could be studied in the other samples (18 in *ultima,* 7 in *ultra,* and 12 in *sivalensis*). Fifteen growth patterns, based on 23 different dimensions, pertain to the dentition, the remainder to the skull (4), jaw (1) and postcranial skeleton (4). The growth gradient in the axial skeleton was evaluated on the basis of central lengths of vertebrae (data from Kernerknecht in Ehrenberg, 1938–1940, which was also the source of most of the data on the appendicular skeleton).

The results are summarized in table 3. The Recent *C. c. crocuta* population was arbitrarily taken as a standard, and all the growth patterns occurring in this sample were denoted "croc." All types found in *spelaea* but not in *crocuta* were denoted "spel," and so on, in a hierarchy arranged on the basis of sample size. It would be most logical to select the ancestral *sivalensis* as a standard, but this is not feasible, as only a part of the characters could be studied in that species.

In some instances, different allometry types were found in local (or temporal) populations of one subspecies. *C. c. crocuta* exhibits two different relationships between blade width and total length of the upper carnassial; the two growth types occur in different regions. In the same way, local samples of *spelaea* are distributed on two different growth patterns regarding width/length of the fourth lower premolar; the differentiation may be temporal or spatial or both. For the great majority of the allometric growth characters, however, perfect intra-specific stability was the rule.

Almost all of the characters show at least one intersample change, except a few which could only be studied in two or three populations. The relationship be-

TABLE 3. *Distribution of allometry types in* Crocuta sivalensis *and four subspecies of* Crocuta crocuta

	y	x	*sivalensis*	*crocuta*	*spelaea*	*ultima*	*ultra*
Skull	L palate*	L skull	croc	croc	croc	croc	—
	W P^4–P^4	L skull	—	croc	spel	spel	—
	W interorbital	L skull	siv	croc	croc	croc	—
	W C–C	W P^4–P^4	siv	croc	croc	croc	—
Jaw	H Processus coronoideus	L C_i—condyle	—	croc	croc	—	—
Axial skeleton	General growth gradient		—	croc	croc	—	—
Limbs	Distal segments	Proximal segments	—	croc	spel	croc	—
	MC & MT I	MC & MT II	—	croc	spel	—	—
	MC & MT II	MC & MT III	—	croc	croc	—	—
Dentition	W P^2	L P^2	siv	croc	croc	croc	croc
	H P^2	L P^2	—	croc	croc	—	—
	W P^3	L P^3	siv?	croc	spel	ultima	siv?
	H P^3	L P^3	—	croc	croc	ultima	—
	L P^4 metacone	L P^4	siv	croc	spel	spel	—
	W P^4 blade	L P^4	spel	croc**	spel	spel	—
	W C_i	L C_i	—	croc	spel	—	—
	W P_2	L P_2	croc	croc	spel	croc?	croc
	H P_2	L P_2	—	croc	croc	croc	—
	W P_3	L P_3	croc	croc	spel	ultima	ultra
	H P_3	L P_3	—	croc	spel	spel	—
	W P_4	L P_4	croc?	croc	spel**	spel†	spel††
	H P_4	L P_4	—	croc	spel	spel?	—
	W M_1	L M_1	siv	croc	spel	spel	croc
	L M_1 trigonid	L M_1	siv	croc	croc	croc	ultra?

* H, height; L, length; W, width.
** Two types in different populations.
† Both *spelaea* types possible.
†† One *spelaea* type excluded.

tween length of palate and length of skull (fig. 3) is the only one which appears to have been stable in all lineages. It could not be studied in *ultra,* but this form links *sivalensis* and *crocuta,* so it is more likely than not to have been similar in this character. On the other hand, there is not a single instance in which all five samples could be shown to differ significantly from each other, though it might be possible to detect such differences if more complete material were available.

The only lineage with three consecutive populations available for study is *sivalensis–ultra–crocuta.* Only seven characters, all in the dentition, could be studied in *ultra;* all of these were also studied in *sivalensis* and *crocuta.* One character (W/L P_2) remains unchanged. In two (W/L P^2, W/L M_1) *ultra* had acquired the *crocuta* pattern; in one (W/L P^3) it retained the *sivalensis* type. In one character (trigonid length/total length M_1) *ultra* is intermediate between *sivalensis* and *crocuta,* indicating that this change occurred in more than one step.

Finally, two characters show more puzzling changes. In one (W/L P_4), *ultra* may agree with one of the types found in *spelaea,* whereas *crocuta* possibly retains the ancestral *sivalensis* pattern, though this inference is somewhat uncertain on account of the small size of the *sivalensis* sample. In another (W/L P_3), *ultra* has a unique allometry pattern, whereas *crocuta,* again, seems to retain the *sivalensis* relationship.

The paleogeographic situation may account for this seeming discrepancy. The known material of *C. c. ultra* represents

the early immigrant population in the extreme south of Africa. It may be thought that this population evolved some distinctive characters during the first colonization, which were later ousted by gene flow from the main population farther northward.

That the allometry changes result from complex genetic changes is clear at once from the unequal distribution of the growth patterns in the five populations; though many of them are identical in several populations, each population has them combined in a different fashion.

On the other hand, morphologically and functionally closely related characters often shift in a correlated way, also within populations, and may thus frequently be affected by the same genes. The functional, and hence selective, advantage of such an arrangement is evident. In the present study, two instances of such functionally and perhaps genetically correlated changes were found. In the limbs of *spelaea* as compared with *crocuta* and *ultima,* the distal segments are shortened, and the proximal lengthened. The change is similar in fore and hind limb, and is not unlikely to have resulted from one or more genetic changes simultaneously affecting the growth gradients in both, in analogy with the well-known case of the Ancon sheep. For this reason fore and hind limb were tabulated together. Another difference between *crocuta* and *spelaea,* possibly with the same kind of correlation, is the change affecting the first digit in both manus and pes, whereas the gradient from the second to the fourth digit remains unaltered. In future this question might be solved by discoveries in the border zone between *crocuta* and *spelaea,* seemingly in the Syria-Palestine region.

Taxonomic Differentiation

To what extent is the differentiation in growth patterns likely to be representative of the actual evolutionary differentiation, i.e. the taxonomic differentiation? The "allometry genes" certainly constitute a very small fraction of the total genome, and the result may have a strong bias. But *a priori* I can see little reason to assume that allometry genes would be either more or less intensively engaged in evolutionary change than any of the genes usually studied experimentally, which, of course, are also a selected group. In one condition it is possible that allometry determinants may be particularly unstable in evolution. This is the case of exceptionally strong allometry (as recorded, for instance, in cats by Kurtén, 1954a). Such growth patterns can only persist unchanged over very short ranges of size, and any sustained evolution in size must be accompanied by some shift of the growth axis, or result in monstrosities. In the present study only two extremely strong allometries were found. One is the axial growth gradient, which is very steep with a growth center in the thoracic region. Nevertheless, this gradient did not change between the small *crocuta* and the large *spelaea,* which in consequence have very different proportions. The differentiation suggested by the "vordere Überbauung" of *spelaea* is thus entirely spurious, and simply a by-product of evolution in size.

The other instance is the steep growth gradient between the first and the second digit in manus and pes, and this did change between *crocuta* and *spelaea,* the change resulting in approximately similar relative proportions: a similarity which is just as spurious as the dissimilarity in the axial skeleton.

The amount of differentiation may now be measured by computing the percentages of different growth types for each population pair (table 4). The results run parallel with the taxonomic arrangement suggested in Kurtén (1956). *Crocuta sivalensis* differs from all subspecies of *C. crocuta* in about 70–80 per cent of the growth patterns studied, whereas the subspecific differences within the latter species are on lower level, modally about 55 per

TABLE 4. *Indices of differentiation for populations of* Crocuta

sivalensis—ultra	71	*crocuta—spelaea*	54
sivalensis—crocuta	67	*crocuta—ultima*	55
sivalensis—spelaea	83	*crocuta—ultra*	57
sivalensis—ultima	75	*spelaea—ultima*	28
ultra—ultima		*spelaea—ultra*	71

cent. There are two exceptions to the latter rule. The differentiation between *C. c. spelaea* and *C. c. ultima* is only on the order of 30 per cent; these two subspecies were probably contiguous in a broad zone. That between *C. c. spelaea* and *C. c. ultra* is great, on the order of 70 per cent, but these two subspecies were both temporally and spatially isolated from each other. That *ultra* belongs in *C. crocuta* is suggested by the figures for that subspecies compared with *crocuta* and *ultima,* which are on the usual subspecific level here found; also, it is just as strongly differentiated from *sivalensis* as are the other *C. crocuta* populations. Geographically, *ultra* and *ultima* are distant, but they are contemporary and close to the point of branching (the migration of *C. crocuta* from India).

DIFFERENTIATION IN OTHER POPULATIONS

The hyena data may be compared with indices for other populations. Table 5 shows the distribution of growth patterns for ten variate pairs in the lower dentition of populations of *Phalanger ursinus,* the bear cuscus of Celebes, based on data from Hooijer (1952). The nominate subspecies inhabits Northern Celebes and Peleng Island; *Ph. u. togianus* lives on the Togean Islands; *Ph. u. furvus* in Central and Southern Celebes. *Ph. u. intermedius* is the name of an extinct subspecies, based on remains from caves in Southwestern Celebes (Hooijer, *op. cit.*). The *ursinus* and *togianus* samples are relatively large, the other two small.

Indices of differentiation are given in table 6; they range from 10 to 70. The slightest differentiation appears to be that between *furvus* and *intermedius,* and it may perhaps be suggested that it does not reach the subspecies level. In fact the published data do not seem to establish differences worthy of subspecies rank.

The *furvus-intermedius* group differs rather strongly from *ursinus* and *togianus;* indices range from 50 to 70. It appears also from Hooijer's paper that this differentiation may be considered the most basic one within the species. On the other hand, Hooijer notes that the character originally used in the separation of *ursinus* and *togianus* (the bicuspid I^3 crown of *togianus*) is unreliable and that these subspecies are not as well separated. The index is, in fact, lower (40) but quite high enough for two subspecies.

Some data, taken from current joint studies by Dr. Robert Rausch and myself on Pleistocene to Recent wolverine and lynx, give further information. Living Alaskan and Fennoscandian wolverine

TABLE 5. *Distribution of growth patterns in populations of* Phalanger ursinus

y	x	*Ph. u. ursinus*	*Ph. u. togianus*	*Ph. u. furvus*	*Ph. u. intermedius*
WP_4	LP_4	U	U	F	F
WM_1	LM_1	U	T	T	T
WM_2	LM_2	U	U	F	F
WM_3	LM_3	U	U	F	F
WM_4	LM_4	U	U	F	F
LP_4	LM_1	U	T	T	T
LM_1	LM_2	U	U	U	U
LM_2	LM_3	U	T	T	I
LM_3	LM_4	U	U	U	U
LM_4	LP_4	U	T	U	U

(the subspecies *Gulo g. luscus* and *Gulo g. gulo*) give the index 43 (on seven cranial and dental characters). A comparison between late Pleistocene and Recent European wolverine gave the index 29; for the living Alaskan compared with the fossil European sample, the index was as low as 14. In each of these cases, the differences in morphology and size seem to warrant subspecific distinction.

A great number of lynx populations could be compared, and the preliminary results are given in table 7. The populations are:

Felis (Lynx) issiodorensis, three samples: (1) from the lower Villafranchian of Etouaires, Mt. Perrier; (2) from the upper Villafranchian of Pardines, Mt. Perrier, from St. Vallier, and the upper Val d'Arno; (3) from the Cromerian of Mauer and Blanzac-Solilhac. The Cromerian form is intermediate between *issiodorensis* and *lynx* and may belong in either, or be a distinct species.

Felis (Lynx) lynx, three samples: a Finnish and a Swedish sample of the nominate subspecies, and a sample of *F. lynx canadensis.*

Felis (Lynx) rufus, three samples from the Californian region, representing the supposed subspecies *F. r. baileyi, F. r. pallescens,* and *F. r. californicus.* These are splitters' subspecies; the differentiation that appears from published data, though real and significant, is in my opinion on an infra-subspecific level.

Data on *Felis rufus,* and on some *F. lynx canadensis,* are from Merriam and Stock (1932).

The *rufus* populations are very slightly differentiated from each other; the index varies between 11 and 17. It may be noted that the Finnish and Swedish demes of *lynx* appear to be more differentiated (index 22). All this is differentiation on the deme level.

On the other hand, the differentiation between Fennoscandian *F. lynx lynx* and North American *F. lynx canadensis* is on the usual subspecies level previously

TABLE 6. *Indices of differentiation for subspecies of* Phalanger ursinus

ursinus—togianus	40
ursinus—furvus	70
ursinus—intermedius	70
togianus—furvus	50
togianus—intermedius	60
furvus—intermedius	10

TABLE 7. *Indices of differentiation for populations of* Felis (Lynx)

	F. lynx lynx, Finland	*F. lynx lynx*, Sweden	*F. lynx canadensis*	*F. rufus baileyi*	*F. rufus pallescens*	*F. rufus californicus*	*F. issiodorensis* Cromerian	*F. issiodorensis* Upper Villafranchian	*F. issiodorensis* Lower Villafranchian
F. issiodorensis Lower Villafranchian	67	67	80	—	—	—	67	6	0
F. issiodorensis Upper Villafranchian	62	62	72	—	—	—	50	0	
F. issiodorensis Cromerian	67	50	67	—	—	—	0		
F. rufus californicus	75	75	67	11	11	0			
F. rufus pallescens	75	75	67	17	0				
F. rufus baileyi	75	75	67	0					
F. lynx canadensis	50	61	0						
F. lynx lynx, Sweden	22	0							
F. lynx lynx, Finland	0								

found, the index varying between 50 and 61. Ellerman and Morrison-Scott do not consider *canadensis* a species separate from *lynx*.

The comparison between two indubitably good species, *F. lynx* (including *canadensis*) and *F. rufus*, gives consistently higher values; they range from 67 to 75. Similarly, the comparison between Recent populations of *lynx* and fossil *issiodorensis* gives somewhat higher values than in the subspecies comparisons. Indices here range from 50 to 80; the range overlaps that of subspecies, but the average is higher.

Finally, the comparison between the fossil samples indicates very slight differentiation between early and late Villafranchian *issiodorensis* (index only 6), but considerably greater between Villafranchian and Cromerian populations. The index thus increases regularly with time, as might be expected, and is on the subspecies level at least, in one instance (67).

Thus the index is again shown to run parallel with the actual taxonomic differentiation. The data may be summarized as in table 8, which gives the statistics for the differentiation index on the deme, subspecies and species levels. With a greater number of raw data, more definite conclusions might probably be drawn, but the table shows some characteristic features of the index and its variation which I believe valid and which deserve comment.

It may first be noted that there seems to be a much greater step from the deme average (11) to that of the subspecies (51) than from the latter to the species (70). But the difference is spurious because of the peculiar nature of the index. It is a geometric series, not an arithmetic, and approaches 100 as a limit; and changes in it should be studied as changes in the expression

$$\log (1 - \text{D.I.}/100)$$

in which D.I. is the differentiation index. If this is done, it is seen that the two steps are very nearly equivalent.

TABLE 8. *Variation of the differentiation index on the deme, subspecies, and species levels*

	N	O.R.	M	σ
Demes	7	0–22	11.0±2.7	7.1±1.9
Subspecies	18	14–71	51.4±3.8	15.7±2.6
Species	22	50–83	70.0±1.5	7.0±1.1

Second, the variation found on the deme level and on the species level appears to be much lower than that on the subspecies level. The difference partly results from the above-mentioned properties of the index; in actual fact the variation for subspecies and species is equivalent. This, of course, indicates that the variation for demes is lower than for subspecies and species. As soon as two demes have attained recognizable differentiation, the taxonomist hastens to elevate them to the rank of subspecies, and this leaves rather little room for differentiation on the deme level.

The equal variation of the index on the subspecies and species level may also seem surprising, until it is remembered that the species that have been compared here are all closely related; more distantly related species would certainly give higher indices. With a very large number of characters it might be possible to follow the index up to the genus level; the data of Reeve and Murray (1942) suggest that some horse genera have identical growth patterns in the skull.

Third, there is a wide overlap of the indices for successive levels. For practical purposes this means that the method is not absolute; the index may help to indicate the taxonomic level of differentiation, but it does not clinch it. Theoretically, it is a link in the chain of evidence showing that the evolution of these species occurred gradually, and not in single steps.

Rates of Evolution

Since this measure of taxonomic differentiation is quantitative, it may be used

TABLE 9. *Rate of evolution of the differentiation index, averaged for 1,000 years*

Ancestor	Descendant	Approximate time lapse	Differentiation per 1,000 years
Crocuta c. ultra	*Crocuta c. crocuta*	500,000 years	0.17%
C. sivalensis	*C. c. crocuta*	1,000,000	0.11
C. sivalensis	*C. c. spelaea*	900,000	0.20
C. sivalensis	*C. c. ultima*	500,000?	0.28
C. sivalensis	*C. c. ultra*	500,000?	0.25
Felis issiodorensis Lower Villafranchian	*Felis lynx*	1,000,000	0.12
F. issiodorensis Cromerian	*F. lynx*	500,000	0.18
Gulo gulo Late-Glacial	*Gulo gulo*	20,000	1.70
Lutra lutra Postglacial	*Lutra lutra*	6,000	0

as a basis for computation of evolutionary rates. It should then be handled as a geometric series.

The results are set forth, in the form of average changes during 1,000 years, within the evolutionary lines that have been studied, in table 9. Let us first consider the rates found in hyenas.

It is unfortunate that only one of the hyena lineages has a reasonably acceptable dating: that from *C. c. ultra* to *C. c. crocuta*.[1] All the others depend on the age of *C. sivalensis,* which cannot be exactly established but probably is on the order of one million years. The influence of an error in this estimate is, of course, greater in the Villafranchian-Cromerian sequence (*sivalensis-ultra, sivalensis-ultima*) than in the Villafranchian to late Pleistocene or Recent sequences (*sivalensis-spelaea, sivalensis-crocuta*). The tabulation is arranged with decreasing accuracy for the time intervals represented, as far as the hyenas are concerned.

The figures are relatively consistent, indicating rates from 0.11 to 0.28 per cent in one thousand years, the average being 0.20. The apparent differences in rate are not significant, though it is entirely possible that the evolution from *C. sivalensis* (with a relatively small population) to Cromerian *C. crocuta* may have been more rapid than the subsequent evolution within that latter, far-flung species. Or there might have been an early Cromerian episode of rapid evolution; this might be suggested by the fact that the Cromerian *ultra* and *ultima,* which are certainly very close to the point of branching, are quite appreciably differentiated. This seems to suggest that the initial differentiation of the subspecies was rapid, and that the average rates of evolution are considerably lower than the rates during the time when the populations conquered new areas and adapted themselves to the new environments.

The fossil lynx populations date from the Villafranchian and the Cromerian. As a basis for rate calculations, I have averaged the indices for each of the fossil populations compared with the three Recent populations of *F. lynx* (Finland, Sweden, and *canadensis*). The indices are: lower Villafranchian, 70.1; upper Villafranchian, 65.3; Cromerian, 60.1. This steady reduction of the index in successive populations suggests a progressive approach to the *F. lynx* type. Morphological studies also indicate that *F. issiodorensis* is ancestral to *F. lynx*. The use of these data for rate estimates is then

[1] The geological dating of *C. c. ultra* as late Cromerian seems to be fairly well established (see Kurtén, 1957), but the absolute age of that interval, taken from the Milankovich-Zeuner chronology, is far from universally accepted.

legitimate, but we are again hampered by the uncertainty regarding absolute ages. Using the same estimates as for the hyenas, we obtain the rates 0.12 (from the lower Villafranchian to Recent) and 0.18 (Cromerian to Recent). The mean, 0.15, is slightly lower than for the hyenas (0.20), but it is of the same order of magnitude.

The comparison between fossil and recent wolverine (*Gulo gulo*) in Europe gives a very different result. The fossil (partly subfossil) sample is very young, dating from the late Paleolithic (later part of last glaciation) and in part even from the earliest postglacial; its mean age may be estimated at about 20,000 years. Here the rate is almost ten times as high as in the previous cases. This is very likely to be a real and important difference. To check on Postglacial evolutionary rates I made a similar study of subfossil to recent Danish otters (*Lutra lutra;* data from Degerböl, 1933).[2] No difference at all was found for this time lapse of about 6,000 years, and the rate as found is zero.

More data of this nature are needed, but what we do have suggests at least that the rate of evolution is variable; the differentiation in the wolverines may represent an "evolutionary spurt" with adaptation to the great changes in the environment which have occurred in postglacial times. For the same period, morphological rates about 400 times as rapid as "normal" or average rates for the group were found in bears by Kurtén (1955). It is quite likely that similar "spurts" have occurred in the histories of hyena and lynx as well, but this will naturally be blurred by the wide temporal spacing of the populations. If so, the normal evolutionary rates would be extremely slow, now and then interrupted by episodes of very rapid evolution—seemingly, in adaptation to changing or newly conquered environments.

[2] This has been included in the computation of average differentiation on the deme level in table 8.

Future study of this type might give increased insight into the problem of rate distributions, first put on a respectable basis by Simpson (1944, 1949, 1953). For such determinations, absolute age data are not necessary; one could, for instance, compare a number of Recent forms with their Cromerian ancestors. But the "spurts" or episodes of rapid evolution can only be pinned down for shorter intervals. The most useful data might be obtained from comparison between latest Pleistocene or early post-glacial populations on one hand and their living descendants on the other.

Conclusions

The index of differentiation, which expresses the percentage of significantly differing growth gradients found in two populations, runs parallel with actual taxonomic differentiation. It may therefore give valuable auxiliary characters in taxonomy.

It may also be used for the study of evolutionary rates. The index increases as a geometric series with the limit value of 100; for instance, the steps from 0 to 50, from 50 to 75, and from 60 to 80, are all equivalent. The average rate of change in the index found in a number of Pleistocene lineages is on the order of 0.2 per thousand years; but in one instance the rate found was as high as 1.7. It is suggested that rates of evolution are very variable. Their distribution might perhaps most profitably be studied in a sample of short-term lineages, for instance in mammals during Postglacial time.

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A MATHEMATICAL MODEL FOR THE CO-EVOLUTION OF OBLIGATE PARASITES AND THEIR HOSTS[1]

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INTRODUCTION

The genetics of disease resistance in plants has been studied by numerous investigators since Biffen first reported in 1905 that host resistance to plant pathogens was a Mendelian character. Although a considerable literature on the genetics of disease resistance has accumulated through the years, the work of Flor, Briggs, and his associates is particularly notable in that a concerted effort has been made to explore the genetic structure of a species in terms of disease resistance. In the present paper, the genetic systems uncovered by the work of Flor, Briggs, and his associates will be briefly reviewed and their evolutionary significance will be interpreted from the standpoint of population genetics.

REVIEW OF LITERATURE

The genetics of pathogenicity and host resistance to flax rust, *Melampsora lini* (Pers) Lev., has been reported by Flor (1955 and 1956). Through a series of genetic studies, Flor has shown that the host and parasite possess complementary genetic systems. That is to say, any gene in the host for resistance acts if and only if there is a corresponding gene in the pathogen for avirulence.

The genes for host resistance exist as a series of multiple alleles at five loci, designated as the K, L, M, N, and P. There is one gene at the K locus, 11 at the L, six at the M, three at the N, and four at the P, making a total of twenty-five genes identified thus far (Flor, 1956). The K, L, and M loci are inherited independently, but the N and P loci are linked with about 26 percent recombination. Unlike the genes for host resistance, the genes for pathogenicity in the pathogen exist at twenty-five separate loci.

Resistance of a host genotype to a particular pathogen genotype occurs whenever any allele in the host (at any one of the five multiple allelic loci) and its complementary gene for avirulence in the pathogen (at any one of the twenty-five diallelic loci) are present simultaneously. The alleles for host resistance are all dominant or semi-dominant so that the heterozygote as well as the homozygote is resistant. The genes for avirulence in the pathogen are also dominant, with the exception of one locus where the homozygous recessive in combination with one or two doses in the host is necessary for resistance. These complementary genetic systems of the host and parasite can best be understood by inspection of the model set forth in table 1. In this model the host has three alleles at one

TABLE 1. *A triallelic-digenic model illustrating the complementary genetic systems of flax and flax rust*

Pathogen Rust phenotype	Host Flax genotype					
	R_1R_1	R_2R_2	R_1R_2	R_1r	R_2r	rr
A_1–A_2–	R	R	R	R	R	S
A_1–a_2a_2	R	S	R	R	S	S
$a_1a_1A_2$–	S	R	R	S	R	S
$a_1a_1a_2a_2$	S	S	S	S	S	S

R—Host resistance and avirulence of the pathogen.

S—Host susceptibility and virulence of the pathogen.

[1] A portion of a thesis submitted to the Graduate Division, Univ. of Calif., Davis, in partial fulfillment of the requirements for the Ph.D. degree.

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locus and the pathogen a pair of alleles at each of two loci. The notation has been adopted from that of Flor (1955), and for the sake of simplicity complete dominance is assumed.

From inspection of table 1 it will be noted that only those host genotypes possessing the R_1 gene are resistant to the pathogen phenotype, A_1–a_2a_2, due to the interaction of gene R_1 in the host and gene A_1 in the pathogen. The recessive host genotype rr, on the other hand, is susceptible to all phenotypes of the pathogen due to the absence of dominant genes for resistance. Likewise, the pathogen genotype, $a_1a_1a_2a_2$, is virulent on all host genotypes due to the absence of dominant genes for avirulence.

An additional feature to be noted from the table is that host genotype, R_1R_2, is resistant to three phenotypes of the pathogen, whereas the other host genotypes possessing dominant genes are resistant to only two. In other words, the presence of two different alleles for host resistance produces an overdominant effect, a necessary condition for the maintenance of stable polymorphism under random mating.

In contrast to the work of Flor, in which both the genetics of the host and parasite were studied, Briggs and his associates have confined their efforts to the genetics of host resistance. Schaller and Briggs (1955a), summarizing the results of long-term investigations on the inheritance of resistance to stinking smut (*Tillitia caries* (DC.) of wheat, report that four genes for disease resistance—H, M, R, and T—belong to the same linkage group. Extensive investigations on the inheritance of resistance to powdery mildew of barley, *Erysiphe graminis hordie* (DC.), have produced similar results. Out of a total of ten genes for mildew resistance identified thus far, five have been found to belong to linkage group II (Schaller and Briggs, 1955b). At one of the five linked loci, at least two alleles for resistance occurs. The genes for resistance to stinking smut of wheat are rather loosely linked, ranging from about a minimum of 15 to a maximum of 37 per cent recombination between two adjacent genes. The genes for resistance to mildew of barley, however, are more tightly linked, the minimum and maximum recombination between two adjacent genes being about 10 and 18 per cent respectively.

From the evolutionary standpoint, at least three questions arise in connection with genetic systems uncovered by the work of Briggs and Flor: (1) What are the consequences of the complementary genetic systems of host and parasite when both the host and parasite mate at random over long periods of time? (2) What is the significance of linkage of genes for disease resistance? (3) What relationship does the genetic systems uncovered by the work of Briggs and Flor bear to the co-evolution of obligate parasites and their hosts? These questions will be considered in turn, but first it is necessary to digress for a moment and discuss some biology of the organisms in question, since a biological understanding of the situation is essential to mathematical arguments that follow.

Biological Considerations

Flax rust is an obligate parasite and cannot survive apart from its host. It is autoecious, i.e., all spore forms are produced on a single host. In mild climates the rust may live from year to year in the uredial or repeating stage, but in more rigorous climates it overwinters as telia on flax straw from the previous season.

The dikaryotic teliospores germinate in the spring and ultimately give rise to haploid sporidia. Sporidial infection of the host plants results in the formation of pycnia of two complementary mating types, plus and minus. Unless a pycnium is fertilized by a pycniospore of the opposite mating type, it is incapable of further development, making the flax rust fungus on obligate outbreeder. A

fertilized pycnium gives a rise to dikaryotic aeciospores, and the aeciospores in turn give rise to the uredial stage which produces a new generation about every ten days. When the fungus is unable to maintain itself in the uredial stage, then, the initiation of each year's infection is concomitant with a sexual-like process. In light of the biology of the flax rust fungus, therefore, it may be treated mathematically as an ordinary diploid organism.

When we consider the evolution of a species from the standpoint of population genetics, the mating system is of prime importance. Since all the host plants in question reproduce by self-fertilization, it is necessary to consider briefly the evolution of selfing systems. There is general agreement among most evolutionists that selfing systems have evolved from previously existing outcrossing systems. Stebbins (1950) states that there is little doubt that the genetic system promoting greater flexibility is the ancestral one; and that self-fertilized types, such as certain annual grasses and herbs, have arisen repeatedly in various phyla and classes in response to selection pressures presumably for immediate fitness.

Throughout this paper we shall assume that such self-fertilized, cultivated annuals as wheat, barley, and flax, like their counterparts in nature, have evolved from open-pollinated ancestors. If this is the case, the genetic structure of these species has evolved for the most part under a system of random mating. Furthermore, it seems reasonable to assume, as suggested by Flor (1955), that such obligate parasites as the rust, smut, and mildew fungi have evolved in association with their hosts. The genetic system of the host and parasite, therefore, have very likely been established in response to two types of opposing selection pressures, namely, the selection pressure exerted on the host by the parasite, and the selection pressure exerted on the parasite by the host. Such selection pressures, acting from remotest antiquity, have very likely resulted in the establishment of genetic systems uncovered by present-day genetic studies. Having disposed of some preliminary biological considerations, we are now ready for a mathematical model of a host-pathogen system.

A Mathematical Model of a Host-Pathogen System

Consider a host-pathogen system in which both the host and parasite mate at random with respect to a single locus in the host and two independent loci in the pathogen. Assume that Flor's complementary genetic systems hold. Let x_1 and x_2 ($x_1 + x_2 = 1$) be the frequencies of genes R_1 and R_2 respectively in the host population, and let y_1, y_2, y_3, and y_4 ($y_1 + y_2 + y_3 + y_4 = 1$) be the frequencies of the gametes A_1A_2, A_1a_2, a_1A_2, and a_1a_2 respectively in the pathogen population.

We shall measure the two opposing selection pressures of the host and parasite in terms of constants analogous to Fisher's (1930) Malthusian parameters. It is assumed that the fitness of the host in a particular host-parasite combination varies inversely as the fitness of the pathogen. That is, if s is the fitness of the pathogen in a particular combination the fitness of the host is a $-$ks. To put it another way, the contributions of offspring of the host and parasite to the next generation are proportional to e^{s} and e^{-ks} respectively. The fitness of the various pathogen genotypes in the vari-

Table 2

Pathogen		Host		
		x_1^2 R_1R_1	$2x_1x_2$ R_1R_2	x_2^2 R_2R_2
y_1^2	$A_1A_1A_2A_2$	s_1	s_1	s_1
$2y_1y_3$	$A_1a_1A_2A_2$	s_2	s_1	s_1
$2y_1y_2$	$A_1A_1A_2a_2$	s_1	s_1	s_2
$2(y_1y_4 + y_2y_3)$	$A_1a_1A_2a_2$	s_2	s_2	s_2
y_2^2	$A_1A_1a_2a_2$	s_1	s_1	s_3
$2y_2y_4$	$A_1a_1a_2a_2$	s_2	s_2	s_3
y_3^2	$a_1a_1A_2A_2$	s_3	s_1	s_1
$2y_3y_4$	$a_1a_1A_2a_2$	s_3	s_2	s_2
y_4^2	$a_1a_1a_1a_1$	s_4	s_4	s_4

ous host-parasite combinations in the proposed system are given in table 2. The fitness of the various host genotypes in a particular combination is obtained by multiplying by $-k$.

The over-all fitness of a particular pathogen genotype is obtained by weighting the fitness of the parasite in each host-pathogen combination by the frequency of the host genotype. Thus the over-all fitness of the pathogen genotype $A_1A_1A_2A_2$ is $s_1(x_1^2 + 2x_1x_2 + x_2^2) = s_1$. Proceeding in the same way, we find the over-all fitness of the host genotype R_1R_1 is $-k[s_1(y_1 + y_2)^2 + 2s_2(y_1 + y_2)(y_3 + y_4) + s_3(y_3^2 + 2y_3y_4) + s_4y_4^2]$.

Continuing in this manner, the two opposing selection pressures of the host and parasite may be presented in tabular form. The selection pressure exerted on the host by the pathogen population is given in table 3; while the selection pressure exerted on the pathogen by the host population is given in table 4.

Under the assumption of continuous generation time, and proceeding in a manner similar to that of Crow and Kimura (1955) and Kimura (1956), the rate of change in the gene and gametic frequencies of the system may be expressed by the set of differential equations:

$$\dot{x}_i = x_i(m_{i.} - \bar{m}) \quad (\text{for } i = 1, 2) \qquad (1)$$
$$\dot{y}_i = y_i(\mu_{i.} - \bar{\mu}) \quad (\text{for } i = 1, 2, 3, 4)$$

TABLE 3

	x_1 R_1	x_2 R_2
x_1R_1	m_{11}	m_{12}
x_2R_2	m_{21}	m_{22}

where

$$m_{11} = -k\{s_1(y_1+y_2)^2 + 2s_2(y_1+y_2)(y_3+y_2) + s_3(y_3^2+2y_3y_4) + s_4y_4^2\}$$
$$m_{12} = m_{21} = -k\{s_1[(y_1+y_2)^2 + 2y_1y_3 + y_3^2] + 2s_2[y_4(y_1+y_2) + y_3(y_2+y_4)] + s_4y_4^2\}$$
$$m_{22} = -k\{s_1(y_1+y_3)^2 + 2s_2(y_1+y_3)(y_2+y_4) + s_3(y_2^2+2y_2y_4) + s_4y_4^2\}$$

TABLE 4

	y_1 A_1A_2	y_2 A_1a_2	y_3 a_1A_2	y_4 a_1a_2
$y_1A_1A_2$	μ_{11}	μ_{12}	μ_{13}	μ_{14}
$y_2A_1a_2$	μ_{21}	μ_{22}	μ_{23}	μ_{24}
$y_3a_1A_2$	μ_{31}	μ_{32}	μ_{33}	μ_{34}
$y_4a_1a_2$	μ_{41}	μ_{42}	μ_{43}	μ_{44}

where

$\mu_{11} = s_1$; $\mu_{12} = \mu_{21} = (1-x_2^2)s_1 + s_2x_2^2$;
$\mu_{13} = \mu_{31} = s_2x_1^2 + (1-x_1^2)s_1$;
$\mu_{14} = \mu_{41} = \mu_{32} = \mu_{23} = s_2$;
$\mu_{22} = (1-x_2^2)s_1 + x_2^2s_3$;
$\mu_{24} = \mu_{42} = (1-x_2^2)s_2 + s_3x_2^2$;
$\mu_{33} = x_1^2s_3 + (1-x_1^2)s_1$;
$\mu_{34} = \mu_{43} = x_1^2s_3 + (1-x_1^2)s_2$, and $\mu_{44} = s_4$

where

$$m_{i.} = \sum_{j=1}^{2} x_j m_{ij}, \quad \bar{m} = \sum_{i=1}^{2}\sum_{j=1}^{2} x_i x_j m_{ij},$$

$$\mu_{i.} = \sum_{j=1}^{4} y_j \mu_{ij}, \quad \bar{\mu} = \sum_{i=1}^{4}\sum_{j=1}^{4} y_i y_j \mu_{ij},$$

and

$$\dot{x}_i = \frac{dx_i}{dt}.$$

At equilibrium the conditions, $\dot{x}_i = 0$ $(i = 1, 2)$ and $\dot{y}_i = 0$ $(i = 1, 2, 3, 4)$, must be satisfied, or equivalently

$$m_{i.} - \bar{m} = 0 \quad (\text{for } i = 1, 2) \qquad (2)$$
$$\mu_{i.} - \bar{\mu} = 0 \quad (\text{for } i = 1, 2, 3, 4)$$

To solve for the gene and gametic frequencies in terms of the parameters of the system is not only difficult but leads to very cumbersome algebraic expressions. A simpler approach is to specify the gene frequencies at equilibrium and then place conditions on the parameters, s_1, s_2, s_3, and s_4. For instance, suppose

the opposing selection pressures are such that the equilibrium $x_1 = x_2 = 1/2$ and $y_1 = y_2 = y_3 = y_4 = 1/4$. Then the parameters of the system must satisfy the equations

$$\begin{aligned} 2s_1 - s_2 - s_3 &= 0 \\ 5s_1 - 2s_2 - s_3 &= 2s_4 \\ 3s_1 - s_2 &= 2s_4 \end{aligned} \tag{3}$$

These equations are not linearly independent, i.e., the first equation is the difference of the latter two and so on. By choosing arbitrary values of two parameters, however, the other two may be determined uniquely by solving any two of the above equations simultaneously.

The next and crucial part of the problem is to obtain the stability conditions for this equilibrium. The methodology for obtaining these conditions has been set forth in detail by Bellman (1953) and has also been used by Kimura (1956). To simplify the argument let x_3 and x_4 be the frequencies of genes A_1 and A_2 respectively in the pathogen population. Then the gametic frequencies become $y_1 = x_3x_4$, $y_2 = x_3(1 - x_4)$, $y_3 = (1 - x_3)x_4$, and $y_4 = (1 - x_3)(1 - x_4)$, and differential equations (1) reduce to the following set of differential equations:

$$\begin{aligned} \dot{x}_1 &= x_1(m_{1.} - \bar{m}) \\ \dot{x}_3 &= \dot{y}_1 + \dot{y}_2 = x_3[x_4\mu_{1.} + (1 - x_4)\mu_{2.} - \bar{\mu}] \\ \dot{x}_4 &= \dot{y}_1 + \dot{y}_3 = x_4[x_3\mu_{1.} + (1 - x_3)\mu_{3.} - \bar{\mu}] \end{aligned} \tag{4}$$

To derive the stability conditions for this equilibrium we begin by evaluating the second differentials of the above equations at equilibrium. Thus in matrix form we have

$$\begin{bmatrix} \delta\dot{x}_1 \\ \delta\dot{x}_3 \\ \delta\dot{x}_4 \end{bmatrix} = \begin{bmatrix} \left(\frac{\partial\dot{x}_1}{\partial x_1}\right)_e & \left(\frac{\partial\dot{x}_1}{\partial x_3}\right)_e & \left(\frac{\partial\dot{x}_1}{\partial x_4}\right)_e \\ \left(\frac{\partial\dot{x}_3}{\partial x_1}\right)_e & \left(\frac{\partial\dot{x}_3}{\partial\dot{x}_3}\right)_e & \left(\frac{\partial\dot{x}_3}{\partial x_4}\right)_e \\ \left(\frac{\partial\dot{x}_4}{\partial x_1}\right)_e & \left(\frac{\partial\dot{x}_4}{\partial x_3}\right)_e & \left(\frac{\partial\dot{x}_4}{\partial x_4}\right)_e \end{bmatrix} \begin{bmatrix} \delta x_1 \\ \delta x_3 \\ \delta x_4 \end{bmatrix}$$

where $(\partial\dot{x}_1/\partial x_1)_e$ means $\partial\dot{x}_1/\partial x_1$ evaluated at equilibrium and so on.

In terms of the parameters of the system, the above equation becomes

$$\begin{bmatrix} \delta\dot{x}_1 \\ \delta\dot{x}_3 \\ \delta\dot{x}_4 \end{bmatrix} = \begin{bmatrix} (\tfrac{7}{16}s_1 + \tfrac{1}{2}s_2 + \tfrac{1}{16}s_4) & -\tfrac{1}{8}(s_1 - s_3) & \tfrac{1}{8}(s_1 - s_3) \\ (\tfrac{1}{8}(s_1 - s_3)) & \tfrac{5}{16}(s_1 - s_2) & \tfrac{1}{16}(\tfrac{3}{2}s_1 - s_2 - \tfrac{3}{2}s_3 + s_4) \\ -\tfrac{1}{8}(s_1 - s_3) & \tfrac{1}{16}(\tfrac{3}{2}s_1 - s_2 - \tfrac{3}{2}s_3 + s_4) & \tfrac{1}{8}(s_1 - \tfrac{1}{2}s_2 - \tfrac{1}{4}s_3) \end{bmatrix} \begin{bmatrix} \delta x_1 \\ \delta x_3 \\ \delta x_4 \end{bmatrix}$$

The necessary and sufficient conditions that the equilibrium be stable is that all solutions of the above equations tend to zero as $t \to \infty$, or that the characteristic roots of the above matrix be negative and real. By straight forward calculations we get the characteristic equation in the following form:

$$\lambda^3 - A\lambda^2 - B\lambda - c = 0$$

where

$$\begin{aligned} A &= a_{11} + a_{22} + a_{33}, \\ B &= a_{12}a_{21} + a_{13}a_{31} + a_{23}a_{32} \\ &\quad - (a_{11}a_{22} + a_{11}a_{33} + a_{22}a_{33}), \\ C &= a_{11}(a_{23}a_{32} - a_{22}a_{23}) \\ &\quad - a_{12}(a_{21}a_{33} - a_{31}a_{23}) \\ &\quad - a_{13}(a_{31}a_{22} - a_{21}a_{32}) \end{aligned}$$

and the a's are the elements of the above matrix, i.e., $a_{11} = \frac{7}{16}s_1 + \frac{1}{2}s_2 + \frac{1}{16}s_4$, $a_{12} = -\frac{1}{8}(s_1 - s_3)$ and so on. The roots of the above cubic equation will be negative and real if and only if $A < 0$, $B < 0$, $C < 0$, and $AB - C > 0$. By specifying values of s_1, s_2, s_3, and s_4, we are in a position to determine the stability of the equilibrium.

For example, suppose we set $s_3 = 0$ and $s_4 = -0.05$, then the simultaneous solution of equations (3) yields $s_1 = -0.10$ and $s_2 = -0.20$. Evaluating the above matrix for these values of s_1, s_2, s_3, and s_4 we find $A = -13/8 < 0$, $B = -67/256 < 0$, $C = -5/2048 < 0$; therefore $AB - C > 0$. Hence, $x_1 = x_2 = x_4 = \frac{1}{2}$ in a stable equilibrium point.

From the mathematical model we see that a host-pathogen system operating under complementary genetic systems of the host and parasite will eventually reach a state of stable equilibrium, providing the above conditions are met. A state of stable equilibrium is advantageous to both the host and parasite. In the first place, a stable pathogen population solves the host's problem of maintenance of resistance to disease, and secondly the pathogen is able to survive without eliminating its host. For, if the genotypes in the pathogen population are not held constant by selection pressure, they will shift in frequency and the more virulent genotypes will finally predominate, resulting in complete susceptibility of the host population. A completely susceptible host population is actually disadvantageous to the pathogen population in the long run. For, under such circumstances, the pathogen tends to eliminate the host and thus eliminates itself in the process. On the other hand, when the opposing selection pressures are such that genes for host resistance and genes for avirulence are held in the system in constant frequency, it is possible for the host and parasite to co-exist over long periods of time. Thus, the problem of the pathogen, existence without eliminating its host, and the problem of the host, the maintenance of resistance to the pathogen, have been solved simultaneously by the complementary genetic systems of the host and parasite.

Linkage of Genes for Disease Resistance

In some situations, linkage of genes for host resistance may also lead to a stable state in a host-pathogen system. For instance, suppose we have a system consisting of three races of the pathogen and two genes for host resistance. Assume the pathogen reproduces asexually, the host reproduces by random mating, and that dominant gene A confers resistance to race α of the pathogen, while gene B confers resistance to race β. Assume further the host population is susceptible to race γ, the third race of the pathogen, but that races α and β predominate race γ by virtue of their superior fitness on susceptible host genotypes.

Now if genes A and B are inherited independently, continued selection against the susceptible genotypes would bring the host population to near homozygosity with respect to genes A and B. This would result in the disappearance of races α and β of the pathogen. But, just as in the case of the complementary genetic systems, the host's problem of maintaining resistance is not solved. For as the frequencies of races α and β diminish, race γ predominates and the host population is completely susceptible to the pathogen.

Next, suppose the dominant genes for resistance are tightly linked in repulsion phase, simulating a single locus system. One of the composite alleles would be of type Ab, the other aB. Two features now become clear. Both homozygotes, Ab/Ab and aB/aB, are susceptible to at least two of the three races; the heterozygote Ab/aB, carrying two genes for resistance, is susceptible to only race γ, the race of low frequency. Under the assumption that the frequencies of the

host genotypes and the fitnesses of races α and β are such that any loss in racial frequency incurred on resistant genotypes is equally balanced by a gain in frequency on susceptible genotypes, it can be shown that such a host-pathogen system would reach a state of stable equilibrium. It should be emphasized, however, that such a state is possible only if a cross-over suppressor, such as a chomosomal inversion, completely inhibits recombination between genes A and B; otherwise the system would be identical to that described above.

It should also be noted that the presence of inversion systems would not necessarily restrict the argument to tight linkage. In fact, two genes may be a considerable distance apart on the chomosome, but as long as they are contained in the inversion they would function as a unit in a population heterozygous for the inversion. If the system of linked genes found in wheat and barley, then, are inversions which have become homozygous when these species evolved from outbreeding to selfing systems, the fact that genes for resistance are separated by several crossover units does not present any serious difficulty to the theory.

Thus we see when the system reaches a state of equilibrium, a host population of intermediate resistance, capable of being maintained over long periods of time, has been substituted for a population of high resistance but of short duration. Under such circumstances, the host population would be better off, in the long run, than if only race γ were present in the system. For the presence of races α and β, by virtue of their superior fitness on susceptible genotypes, would tend to keep new races which arise by mutation in check, since another race would gain ascendency in the system only if its fitness were greater than that of α and β. Hence, the host would not have to cope with rapid race shifts in the pathogen. If a highly virulent race did arise through mutation, however, it would eventually supplant the existing races and the system would degenerate and again the host would have to evolve another defensive mechanism for its survival.

Evolutionary Significance

If the arguments which have just been advanced approximate reality, the evolutionary significance of the genetic systems uncovered by the work of Briggs and Flor becomes clear. They are the relics of ancient systems of balanced polymorphism, stemming from the time wheat, barley and flax reproduced by outbreeding. In the final analysis, it seems quite plausible that these dual systems of balanced polymorphism, one in the host population the other in the pathogen population and due either to complementary genetic systems of the host and parasite or to linked genes for host resistance, have provided the mechanism for the co-evolution of obligate parasites and their hosts. Indeed, it seems quite likely that some such state of balance and equilibrium was a necessary condition for this co-evolution.

Summary

A mathematical model of a host-pathogen system was presented and a theory of the evolutionary significance of the genetic systems uncovered by the work of Briggs and Flor was proposed. It was suggested that these genetic systems uncovered by present day genetic studies are the relics of ancient systems of balanced polymorphism, stemming from the time wheat, barley, and flax reproduced by outbreeding. It was further suggested that a state of dual balanced polymorphism was a necessary condition for the co-evolution of obligate parasites and their hosts.

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GEOGRAPHIC ISOLATION AND PHENOTYPTIC CONSTITUTION OF POPULATIONS OF *LEPIDOBATRACHUS ASPER*, A NEOTROPICAL BATRACHIAN INHABITANT OF ARID REGIONS

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Introduction

The purpose of this article is to record a remarkable case of geographic isolation and of its effects on the structure of populations of a species. A small isolated population presents a strong contrast with much more variable populations of the same species which inhabit far more extensive territories. The species in question is *Lepidobatrachus asper,* a ceratofridean inhabitant of the biocenoses of Gran Chaco in Argentina. This form belongs to an apparently ancient family, endemic to the Neotropical region. *L. asper* is the only known species of its genus; the "species" *L. laevis* distinguished by Budgett (1899) has been shown to be merely a seasonal variant (Paz, 1955). This amphibian is a chiefly terrestial burrowing form, which lives in temporary shallow lagoons only during the reproductive season which coincides with the period of summer rains. The animals are nocturnal, voracious, and cannibalistic. Some populations are, as will be described below, distinguished by their aggressivity, which is absent in other populations.

Geographic Distribution

The geographic distribution of *Lepidobatrachus asper* is shown in figure 1. This species occupies rather extensive territories of Chaco Boreal and Chaco Central, in the Province of Formosa, Argentina. The populations of those territories are quite variable morphologically. Farther to the south, in Argentina, are found two narrowly localized populations of the same species, which are much less variable (Cei, 1955). The habitats of these latter populations are: (1) Llanos de La Rioja, with clay soil and a xerophytic, probably relictual, vegetation, and (2) the salt flats of Santiago del Estero (Saladillo), with a specialized halophytic vegetation. The populations of Santiago del Estero are characterized by their small body size (3.5 to 4.5 cm body length in adult individuals); this is apparently a true case of dwarfism. This population is insufficiently known, and it will not be considered further in the present article.

Morphology

Morphological traits which distinguish populations of *Lepidobatrachus asper* have been described by Vellard (1948). Those particularly useful for the present study are the following indexes:

1) Head shape, measured by the ratio distance from the snout to the tympanal line: tympanal line (distance between the centers of the tympani) (fig. 3).

2) Position of the nostrils (measured by the ratio distance from the nostril to the eye): diameter of the eye (fig. 4).

3) Position of the eyes (measured by the ratio distance between the eyes): eyelid diameter (fig. 5).

Other indexes used by systematists, such as tibia: body length; tympanum: head length; tympanum diameter, etc., are less useful for our purposes.

FIG. 1. Geographic distribution of *Lepidobatrachus asper*. 1. Chaco populations. 2. Saladillos salt plains population. 3. La Rioja population.

The material examined is in the collections of the Instituto M. Lillo, at Tucuman, and consists of 134 individuals (adults) from northern and central Gran Chaco (Hickman, Salta; Ing. Juarez and Puerto Irigoyen, Formosa), and 23 individuals (also adults) from the Llanos de La Rioja. The diagrams in figures 3, 4, and 5 represent the observed distributions of the indexes indicated above, the vertical axis giving the observed frequencies in percentages. The entire material of the Gran Chaco origin is treated jointly, since the samples from the different localities appear to be uniform. Similarly, the material from La Rioja is treated as a unit. No sexual dimorphism in some indexes (table 1) (i.e. head shape) has been noted in any of the populations.

Examination of the figures shows that the populations of Gran Chaco differ quite significantly from those of La Rioja. It also shows that specially the Gran Chaco populations show a tendency towards

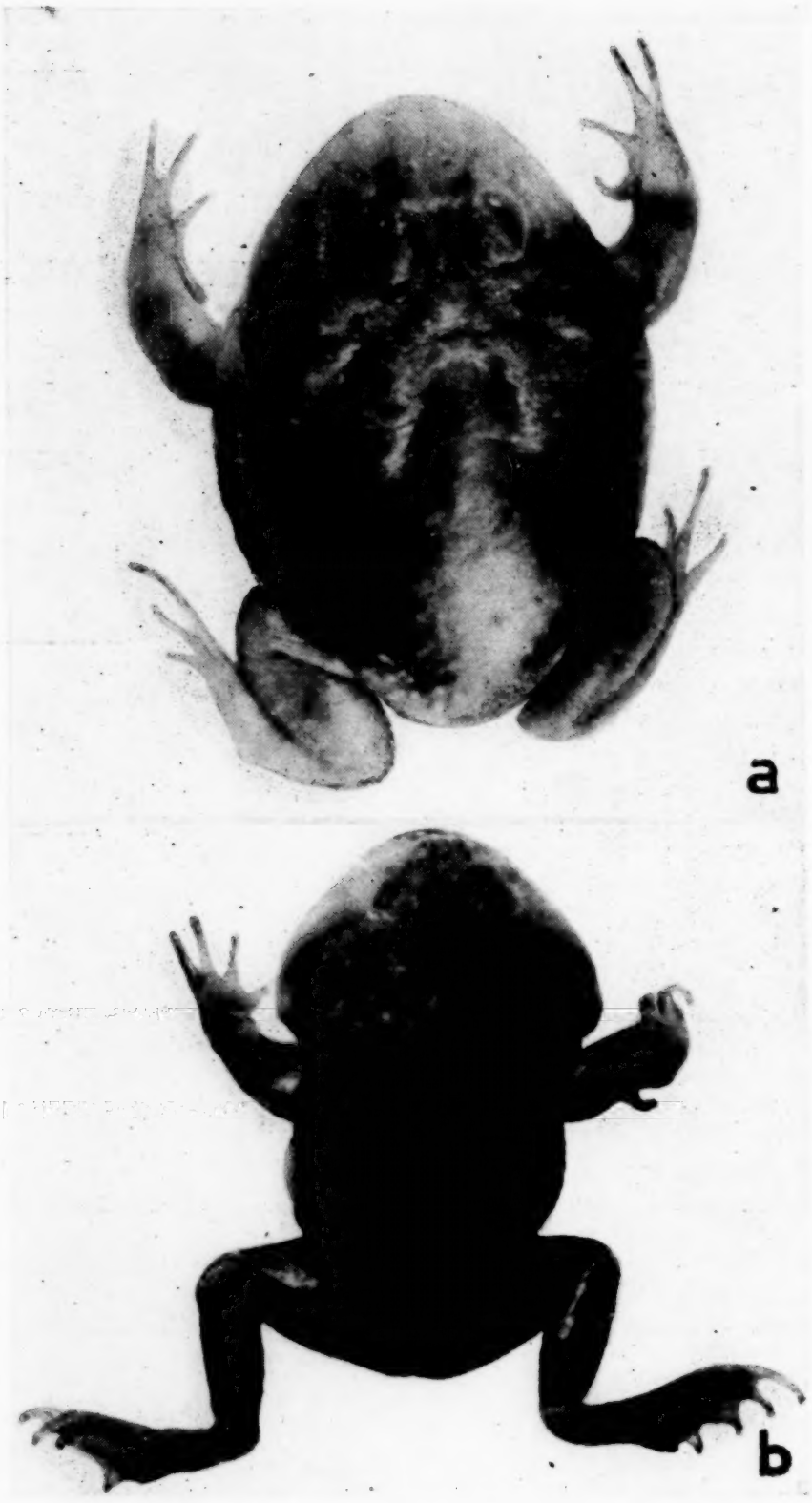

FIG. 2. Male specimens of *Lepidobatrachus asper* from Argentina: a) "long head" Central Chaco population; b) "short head" La Rioja population.

intrapopulational polymorphism, some curves showing a more or less distinct bimodality. To emphasize this latter point, we may use indexes below 76 to characterize individuals with a "short head," and above 76 the trait "long head." Similarly we may distinguish prognathous individuals (index below 85) and orthognatous individuals (index above 85), and individuals with eyes close (index below 90) and those with well separated eyes (index above 90). The "short head" is found in 35.5% of individuals from Gran Chaco but in 69.5% of those from La

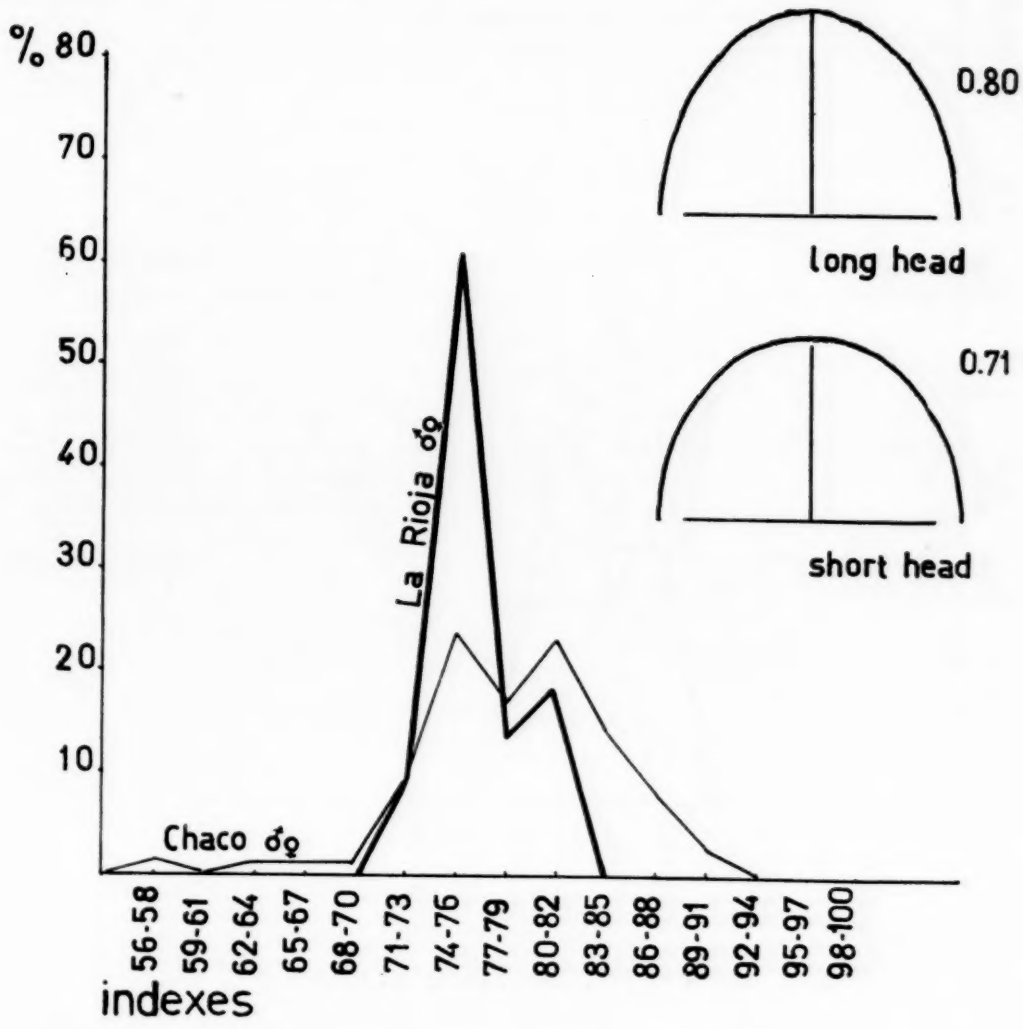

FIG. 3. Index of head shape: tympanal line.

Rioja; the orthognatism occurs in 29.8% of individuals in Gran Chaco and 69.5% in La Rioja; and separated eyes are observed in only 8.2% of individuals in Gran Chaco and 88.2% in La Rioja.

The geographic isolation in the specialized environment of La Rioja has, then, resulted in formation of a very distinctive local race. The La Rioja race can be characterized as consisting of individuals mostly with short heads, orthognatism, and separated eyes, and also by a smaller and less variable size (mean 7.3 cm, limits 6.3–8.7 cm), and by a reddish ochraceous dorsal coloration with brilliant orange-yellow axillary spots. Personal field observations in April of 1951 and February 1952 have also shown that the animals of the La Rioja race lack the characteristic aggressive behavior of the Gran Chaco race (Cei, 1955). The populations of Gran Chaco consist chiefly of individuals with long heads, prognatism, and close eyes, these traits being associated with a greater and more variable size (mean 7.8 cm, limits 5.1–12.3 cm), a variable coloration but less evident axillary spots, and a very aggressive behavior (Cei, 1955). The traits non-aggressive vs. aggressive behavior refer to the immediate reaction of the animals to external stimuli. In the Gran Chaco populations, individuals react to any provocation almost instantaneously by inflating themselves, emitting a hissing sound like an infuriated cat, and by passing to attack the adversary by jumping and biting him. Individuals from La Rioja, on the contrary, do not respond to provocation, inflate themselves only a little, emit no

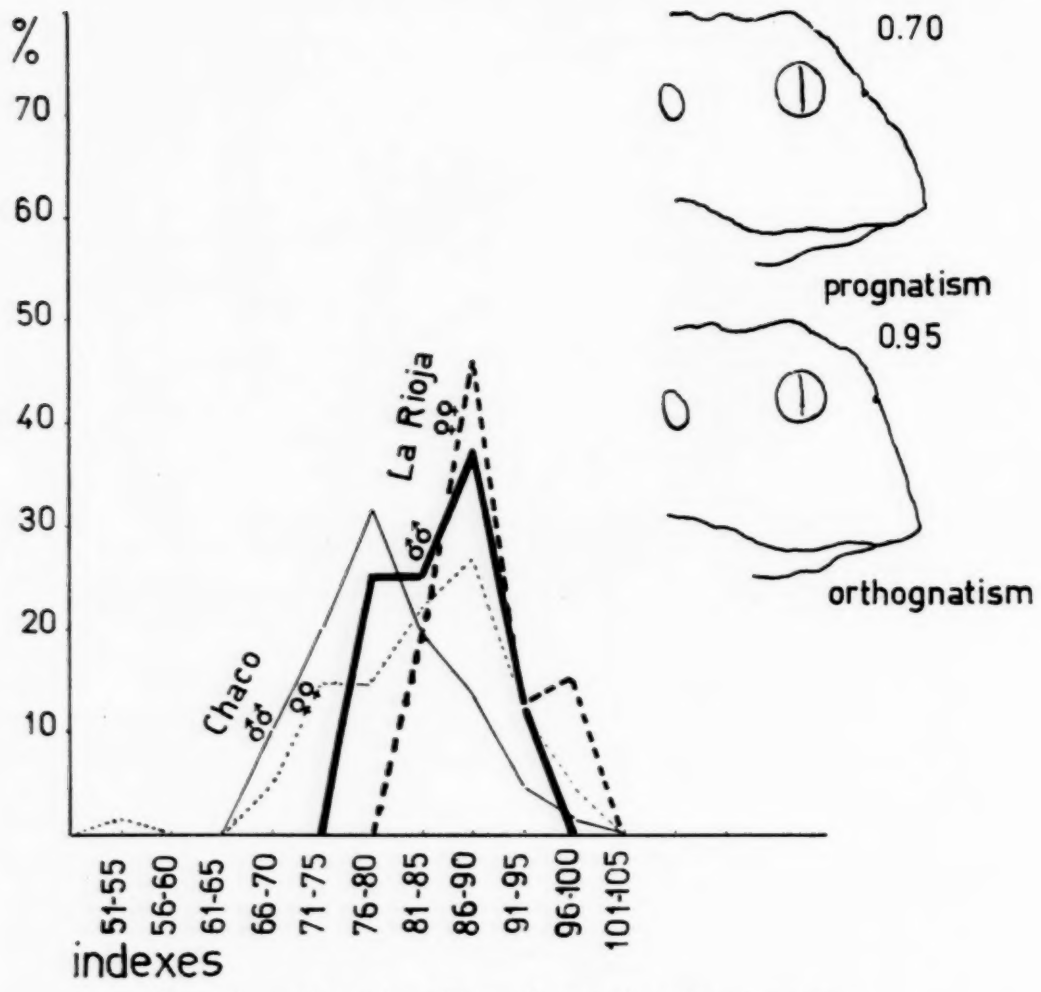

FIG. 4. Index of position of nostrils: diameter of eye.

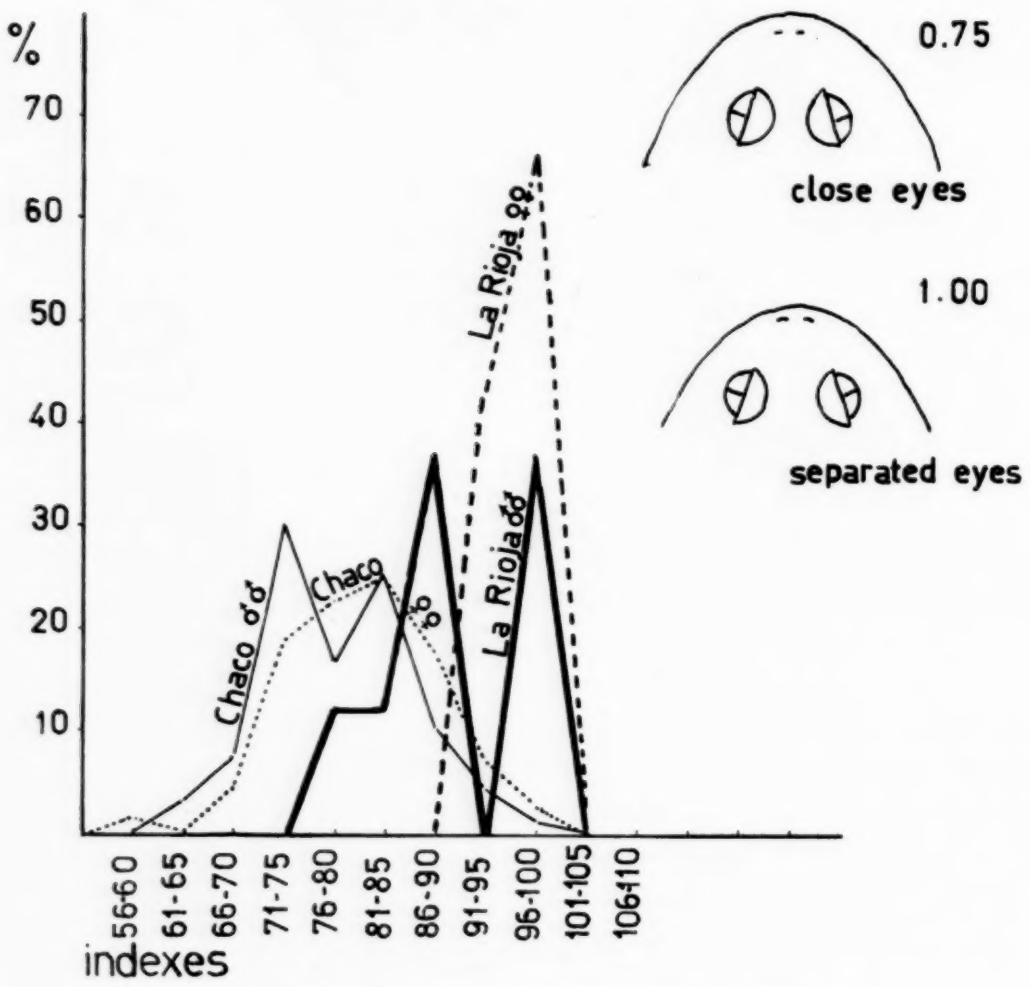

FIG. 5. Index of position of eyes: eyelid diameter.

TABLE 1. *Indexes used in comparisons*

Indexes:				
1—Head shape				
66 ♂♂	Chaco	M = 79.09 ± 6.02	t = 0.01,	P = 0.90–1
68 ♀♀	Chaco	M = 78.98 ± 4.71		
8 ♂♂	La Rioja	M = 77.00 ± 3.02	t = 0.08,	P = 0.90–1
15 ♀♀	La Rioja	M = 75.93 ± 2.09		
8 ♂♂	La Rioja	M = 77.00	t = 1.60,	P = 0.10–0.20
66 ♂♂	Chaco	M = 79.09		
15 ♀♀	La Rioja	M = 75.93	t = 3.86,	P = 0.01–0.001
68 ♀♀	Chaco	M = 78.98		
2—Position of the nostrils				
66 ♂♂	Chaco	M = 79.84 ± 7.14	t = 2.45,	P = 0.01–0.02
68 ♀♀	Chaco	M = 83.13 ± 8.35		
8 ♂♂	La Rioja	M = 84.00 ± 5.70	t = 2.57,	P = 0.02–0.05
15 ♀♀	La Rioja	M = 90.60 ± 6.10		
8 ♂♂	La Rioja	M = 84.00	t = 5.07,	P < 0.001
66 ♂♂	Chaco	M = 79.84		
15 ♀♀	La Rioja	M = 90.60	t = 3.97,	P = 0.001–0.01
68 ♀♀	Chaco	M = 83.13		
3—Position of the eyes				
66 ♂♂	Chaco	M = 78.24 ± 8.00	t = 1.24,	P = 0.20–0.30
68 ♀♀	Chaco	M = 81.07 ± 7.70		
8 ♂♂	La Rioja	M = 89.87 ± 7.11	t = 2.62,	P = 0.02–0.05
15 ♀♀	La Rioja	M = 96.86 ± 3.31		
8 ♂♂	La Rioja	M = 89.87	t = 4.30,	P = 0.001–0.01
66 ♂♂	Chaco	M = 78.24		
15 ♀♀	La Rioja	M = 96.86	t = 12.53,	P < 0.001
68 ♀♀	Chaco	M = 81.07		
—Size (en mm.)				
66 ♂♂	Chaco	M = 73.66 ± 11.70	(Range 51–98)	
8 ♂♂	La Rioja	M = 68.62 ± 2.67	(Range 65–72)	
68 ♀♀	Chaco	M = 82.27 ± 16.00	(Range 60–123)	
15 ♀♀	La Rioja	M = 75.20 ± 5.47	(Range 63–87)	
♂♀	Chaco:	t = 3.56,	P < 0.001	
♂♀	La Rioja:	t = 3.86,	P = 0.001–0.01	
♂♂	Chaco-La Rioja:	t = 2.93,	P = 0.01–0.02	
♀♀	Chaco-La Rioja:	t = 2.90,	P = 0.01–0.02	

sound, and do not attack. This ethological trait, non-agressive behavior, is uncommon among the Ceratophridae. In this family, the species of Ceratophrys, Stombus, and Lepidobatrachus are all very aggressive in response to stimuli, and only the Odontophrynus species do not show this aggressivity.

DISCUSSION

The isolated population of the Llanos de La Rioja shows remarkable morphological and behavioral differences from the populations of Gran Chaco. Owing to difficulties in raising the progenies from experimental crosses of these animals, it

has not been possible to establish which of the contrasting traits of the La Rioja and Gran Chaco populations are dominant and which are recessive. This being the case, an attempt to express the differences between these populations in terms of gene frequencies would be premature. It is possible that the La Rioja colony consists mostly of homozygotes, while the Gran Chaco populations are polymorphic.

The arid "llanos" of La Rioja show some characteristics of the Chacoan biocenoses. However, the La Rioja ecological formations are isolated from those of Gran Chaco (woods of Schinopsis) by the mountains of the Sierra de La Rioja and by extensive salt flats. Some of these isolating barriers are quite ancient, corresponding to the area submerged during the last marine transgression of the Tertiary ("the entrerrian stage"). For the time being it is not known whether the differences observed between the races of *Lepidobatrachus asper* are adaptive to the environments of the respective races. The race of La Rioja shows a combination of traits—a short orthognatous head, a rather constant coloration and body size, and the absence of aggressiveness. It is possible that all these traits are physiologically and genetically correlated.

Summary

Lepidobatrachus asper is a species widespread in Gran Chaco. An isolated population of this species living in La Rioja differs greatly from the Gran Chaco populations. In Gran Chaco, the animals are characteristically long-headed, prognatous, close-eyed, large-bodied, variable in coloration, and markedly aggressive in behavior. The La Rioja individuals are short-headed, orthognatous, with separated eyes, small-bodied, uniformly colored, and non-aggressive. The differences may represent an extreme case of genetic divergence of geographically isolated populations.

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CHROMOSOME NUMBERS AND EVOLUTION IN THE GENUS *COLCHICUM*

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The main chromosome studies in *Colchicum* (Liliaceae) have been published by Levan (1940) and by D'Amato (1955, 1956, 1957). Taking into account the findings published in this paper, chromosome numbers are known for 21 out of 64 species of *Colchicum* (excluding *Merendera* and *Bulbocodium*). Before a clearer picture of the chromosome evolution within *Colchicum* can emerge, more counts will have to be made, especially of material from the main diversity centre of the genus, i.e. N. Syria, Asia Minor and the Balcan Peninsula. However, tentative ideas on some evolutionary trends within the genus seem to be justified at this stage.

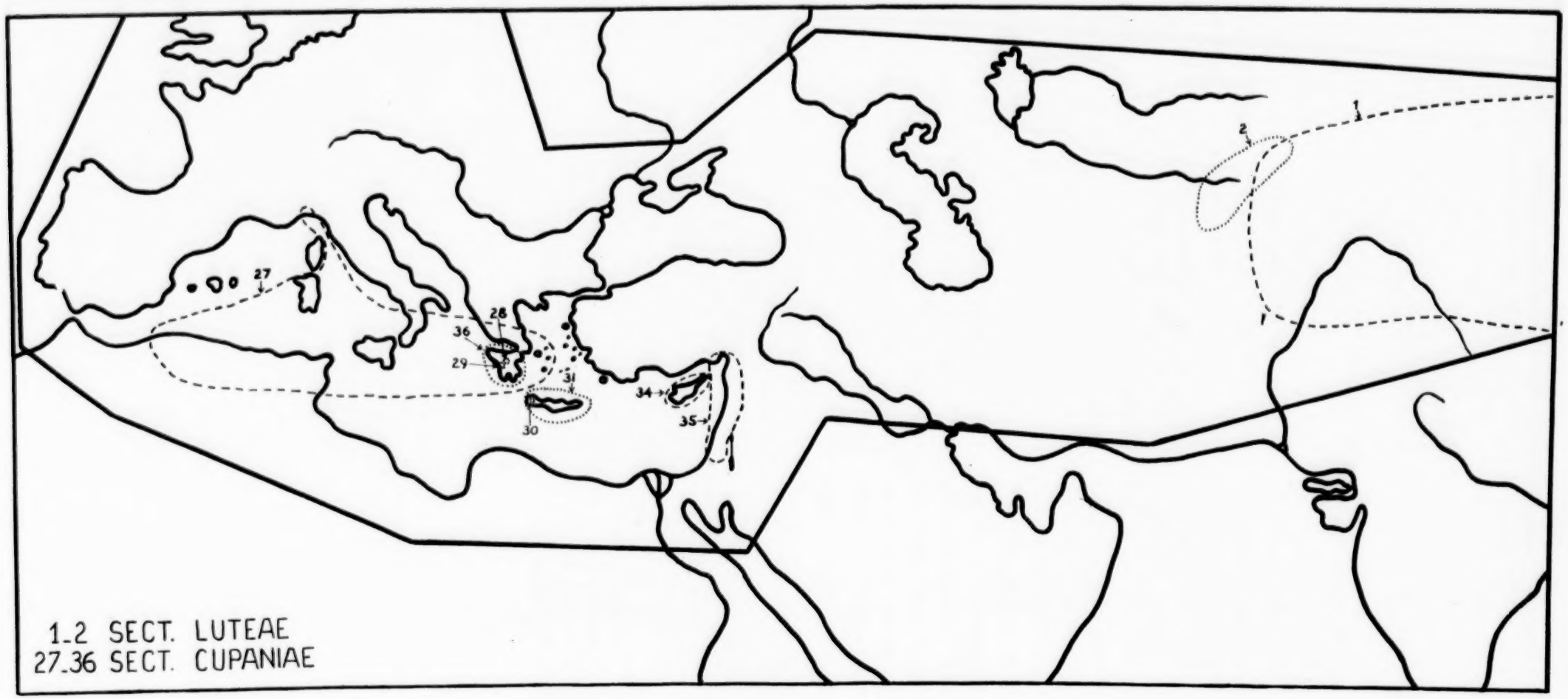
MATERIAL AND METHODS

The somatic chromosomes of nine *Colchicum* species, seven of them from Palestine, one from Cyprus and one from Sinai, have been investigated. These nine species belong to three different sections, namely, Sect. Bulbocodiae, Sect. Cupaniae and Sect. Autumnales, according to the classification of Stefanoff (1926), the monographer of the genus. The root-tips of corms, collected in natural habitats, were squashed after pretreatment in either 8-Oxychinoline or α-Monobromonaphthalene (MBN) and stained in aceto-orceine or in Feulgen's leucobasic fuchsin. Details of the treatment of each species, as well as of the origin of the plants studied are given in table 1.

Colchicum is known to be a difficult material for chromosome studies, and almost every author who dealt with *Colchicum* mentions this fact. The main difficulty met with in this study was the lack

TABLE 1. *Material studied*

No.	Species	2n	Pre-treatment	Fixing fluid	Stain	Origin of plant
1.	*C. schimperi* Janka	14	a. Oxychinoline 3 h.	No fixation	Aceto-orcein	Negev, Wadi Rammon
			b. Mono-bromo-naphthalene 2½ h.	Acetic alcohol		Negev, Wadi Rammon
2.	*C. ritchii* R. Br.	14	a. MBN 3½ h.	Acetic alcohol	Aceto-orcein	Negev, Revivim
			b. Oxychinoline 3 h.	Acetic alcohol	Feulgen	Negev, S. of Beersheva
3.	*C. tuviae* Feinbr.	14	MBN 3½ h.	Acetic alcohol	Aceto-orcein	Negev, Beersheva
4.	*C. guessfeldtianum* Asch. et Schw.	14	MBN 3½ h.	Acetic alcohol	Aceto-orcein	Sinai Penins., Jebel Maghara
5.	*C. steveni* Kth.	54	MBN 3 h.	Lewitsky	Feulgen	Jerusalem
6.	*C. hiemale* Freyn	54	MBN 3½ h.	Acetic alcohol	Aceto-orcein	Cyprus, Nicosia
7.	*C. hierosolymitanum* Feinbr.	18	a. MBN 2½ h.	Lewitsky	Feulgen	Jerusalem
			b. Oxychinoline 4 h.	Acetic alcohol	Aceto-orcein	Jerusalem
			c. MBN 3½ h.	Acetic alcohol	Aceto-orcein	Jerusalem
8.	*C. decaisnei* Boiss.	54	MBN 1 h.	Lewitsky	Feulgen	Upper Galilee
9.	*C. tunicatum* Feinbr.	54	MBN 2½ h.	Lewitsky	Feulgen	Negev hills, S. of Beersheva



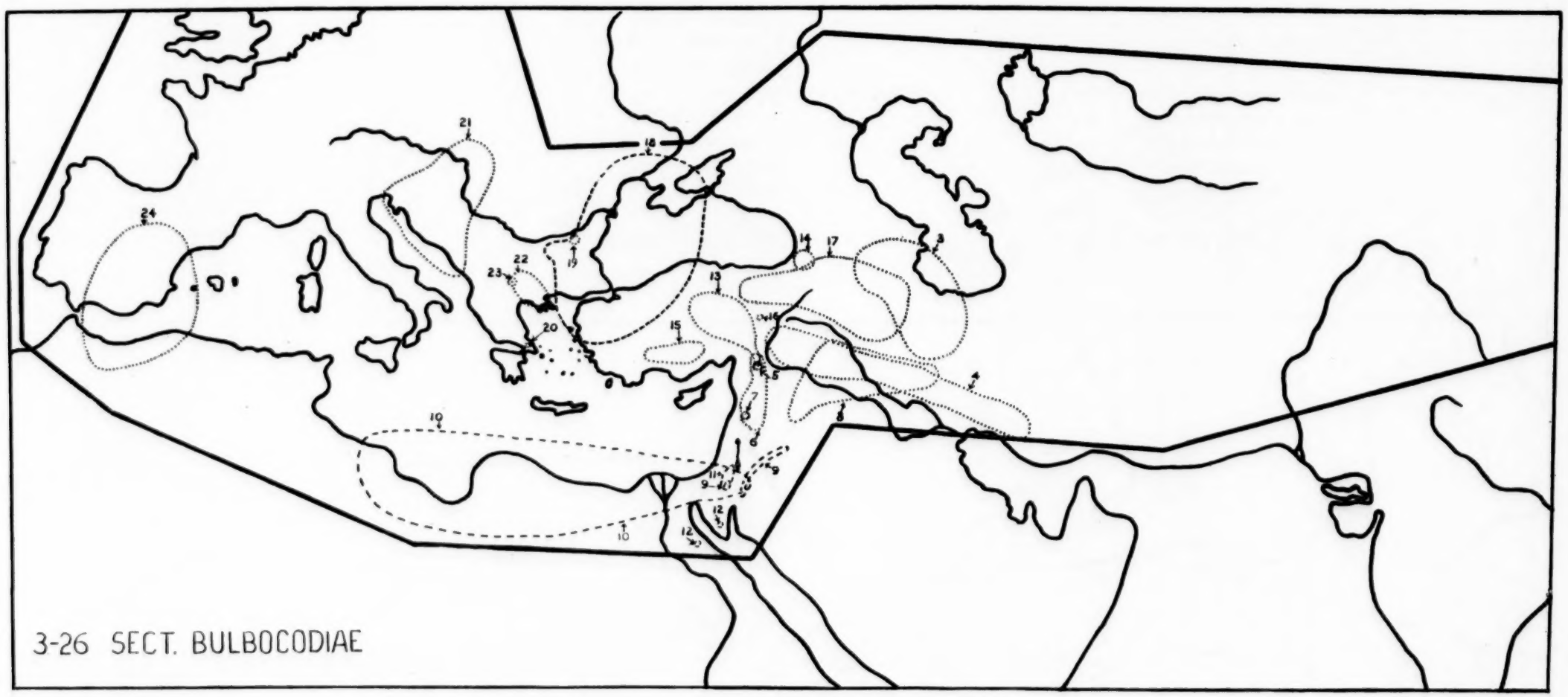
a

FIG. 1. Maps showing distribution patterns.

Section. Luteae Stef.
1. *C. luteum* Bak.
2. *C. kesselringii* Reg.

Section. Cupaniae Stef.
27. *C. cupani* Guss.
28. *C. psaridis* Heldr.
29. *C. boissieri* Orph.
30. *C. creticum* Turrill
31. *C. pusillum* Sieb.

32. *C. peloponesiacum* Rech. f. et Davis
33. *C. andrium* Rech. f. et Davis
34. *C. hiemale* Freyn
35. *C. steveni* Kth.
36. *C. parlatoris* Orph.

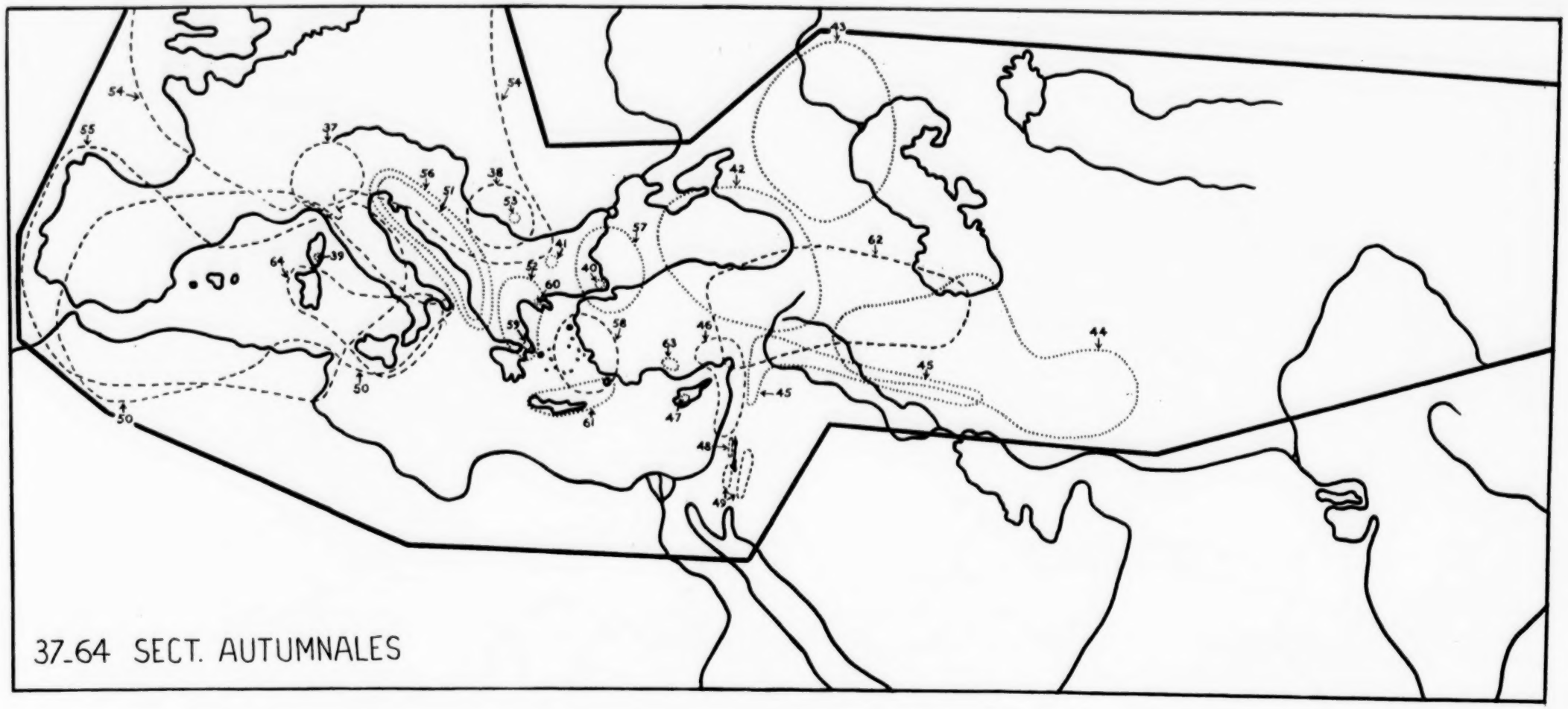


b

Section. Bulbocodiae Stef.

3. *C. szowitsii* F. M.
4. *C. crocifolium* Boiss.
5. *C. fasciculare* Boiss.
6. *C. brachyphyllum* Boiss.
7. *C. libanoticum* Ehr.
8. *C. deserti-syriaci* Feinbr.
9. *C. schimperi* Janka
10. *C. ritchii* R. Br.
11. *C. tuviae* Feinbr.
12. *C. guessfeldtianum* Asch. et Schw.
13. *C. tauri* Siehe
14. *C. serpentinum* Wor. ex Misc.
15. *C. hydrophilum* Siehe
16. *C. hirsutum* Stef.
17. *C. bifolium* Freyn et Sint. (=*C. nivale* Boiss. et Huet)
18. *C. ancyrense* Burtt (=*C. biebersteinii* Rouy)
19. *C. davidovi* Stef.
20. *C. catacuzenium* Heldr.
21. *C. hungaricum* Janka
22. *C. dörfleri* Hal.
23. *C. macedonicum* Koš.
24. *C. triphyllum* Kze.
*25. *C. jezdianum* Czern.
*26. *C. palmetorum* Czern.

* Areas of 25. C. jezdianum and 26. C. palmetorum are not marked on the map.



c

Section. Autumnales Stef.

37. *C. alpinum* Lam. et DC.
38. *C. arenarium* W. K.
39. *C. corsicum* Bak.
40. *C. micranthum* Boiss.
41. *C. borisii* Stef.
42. *C. umbrosum* Stev.
43. *C. laetum* Stev.
44. *C. kotschyi* Boiss.
45. *C. haussknechtii* Boiss.
46. *C. decaisnei* Boiss.
47. *C. troodi* Ky.
48. *C. hierosolymitanum* Feinbr.
49. *C. tunicatum* Feinbr.
50. *C. neapolitanum* Ten.
51. *C. kochii* Parl.
52. *C. lingulatum* Boiss. et Sprun.
53. *C. haynaldii* Heuff.
54. *C. autumnale* L.
55. *C. lusitanum* Brot.
56. *C. visianii* Parl.
57. *C. orientale* Frivaldsky ex Kth. (= *C. turcicum* Janka)
58. *C. variegatum* L.
59. *C. sibthorpii* Bak.
60. *C. bowlesianum* Burtt
61. *C. macrophyllum* Burtt
62. *C. speciosum* Stev.
63. *C. cilicicum* Dammer
64. *C. bivonae* Guss.

of uniformity in results obtained with different species after similar treatment. In some of the species chromosomes stained faintly, in others they failed to scatter, in still others they failed to show their primary constrictions, etc. However, none of the prominent stickiness mentioned by various authors was observed.

Results

Sect. Bulbocodiae Stef.

Four species of this section, characterised by flowering after the emergence of leaves, have been studied: *C. schimperi, C. ritchii, C. tuviae* and *C. guessfeldtianum.* These represent a group of desert or steppe plants in the southeastern part of the *Colchicum* area (see map b, fig. 1). The four species occupy different ecological niches and can be well distinguished morphologically (for details on their taxonomy and ecology see Feinbrun, 1953). Their respective geographical areas are more or less continuous or even slightly overlapping.

Three species of this group (*C. ritchii, C. tuviae* and *C. guessfeldtianum*) display

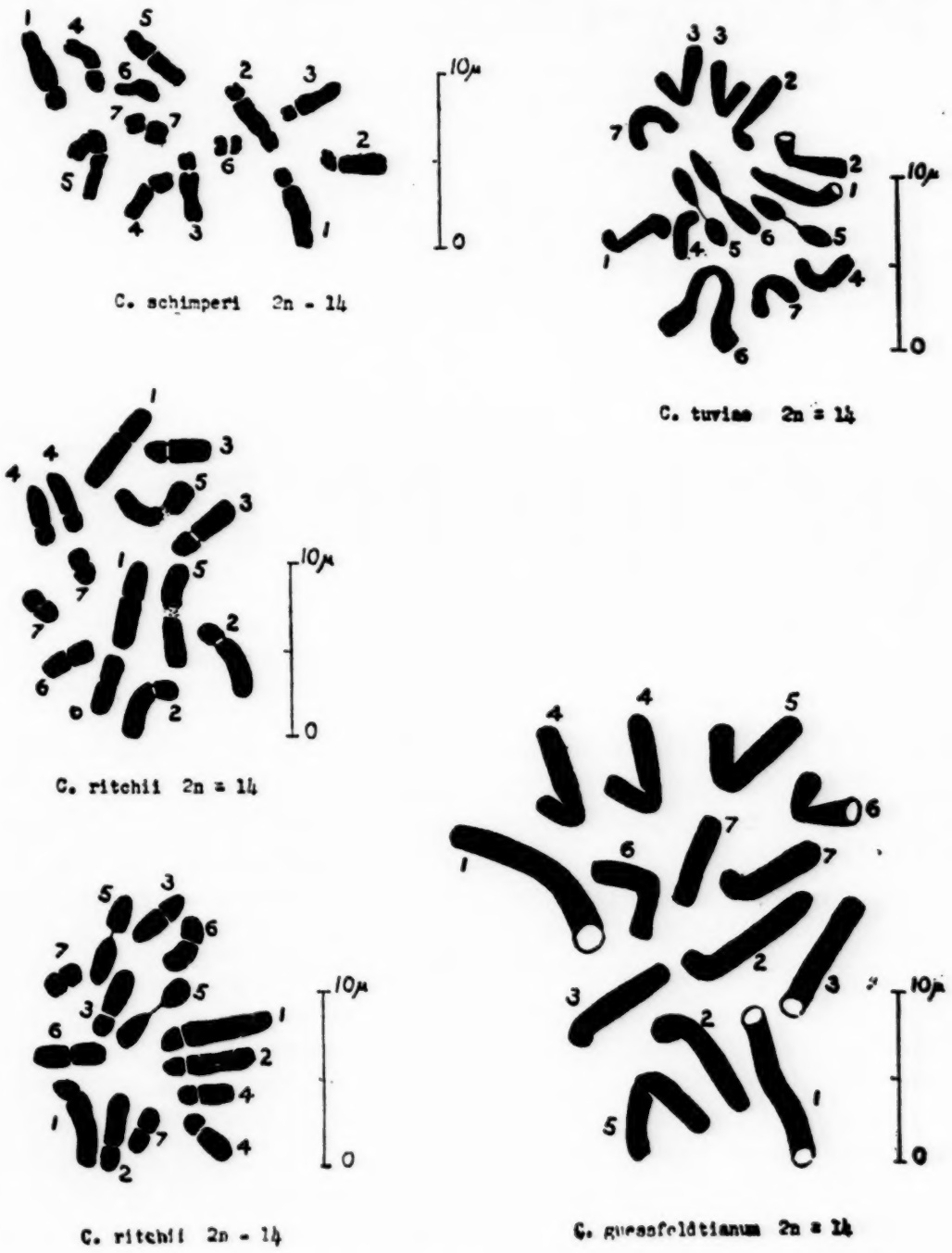


FIG. 2. Somatic metaphase plates of four species belonging to the Bulbocodiae section.

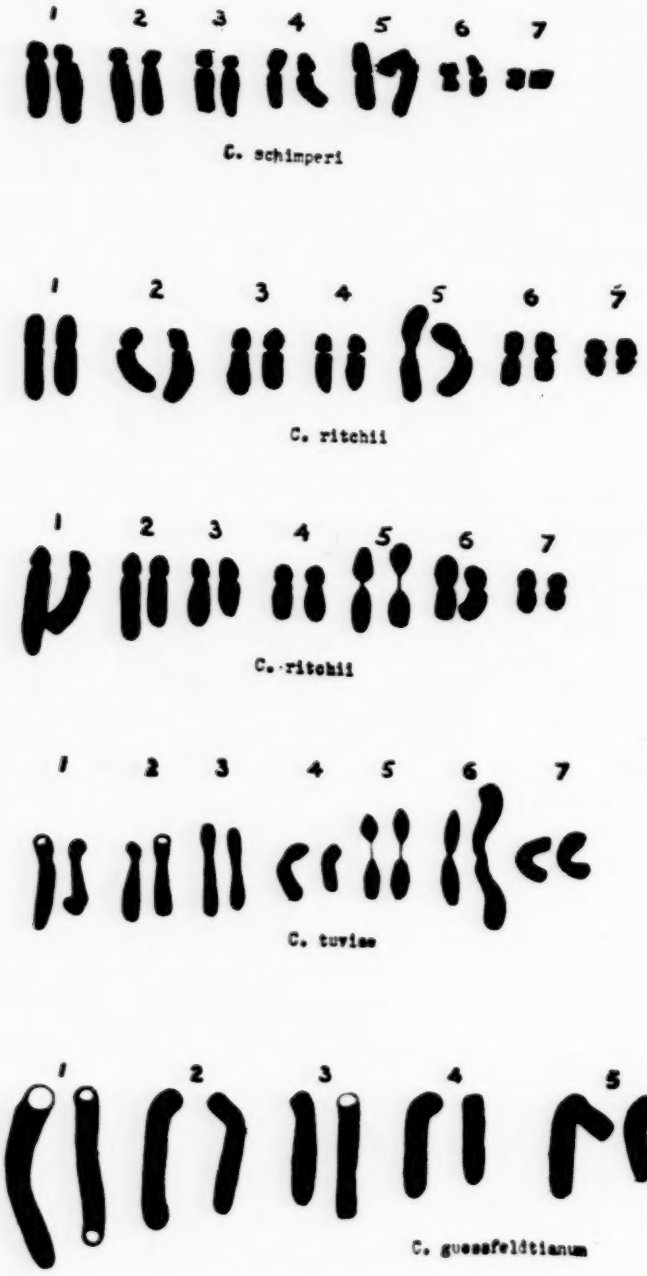


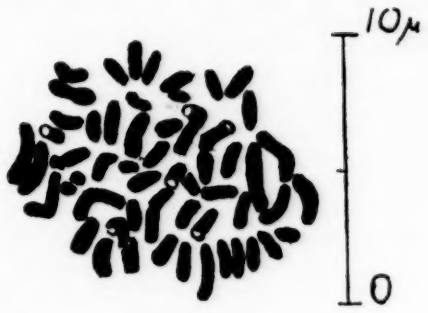
FIG. 3. Idiograms of the four Bulbocodiae species.

in their flowers a peculiar characteristic, rare in this section and absent in all other *Colchicum* sections, namely, the presence of toothed ridges on the segments of the perigonium on either side of the filament. In *C. ritchii* and *C. guessfeldtianum* these occur on the outer segments only, while in *C. tuviae,* where the teeth are longest and much more numerous, they occur on both the outer and inner ones.

The chromosome number found in the above species of this group is $2n = 14$ (figs. 2, 3), which is the lowest number found so far in *Colchicum*. Thus, $x = 7$ can be given as a basic number for the genus.

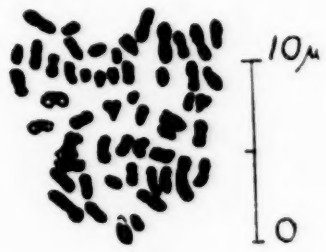
C. schimperi and *C. ritchii* resemble each other in their chromosome morphology. Their karyotypes comprise four chromosome pairs, gradually diminishing in length, with a subterminal centromere (designated by numbers 1–4); one pair (designated 5) with a median, peculiarly long centromere; and two small pairs (6, 7) with a median centromere.

The karyotype of *C. tuviae* differs from the above by the prominently larger chromosome 6. The chromosomes of *C. guessfeldtianum* examined appeared vacuolated and swelled, but owing to scarcity of material no additional preparations could be obtained. However, except for larger

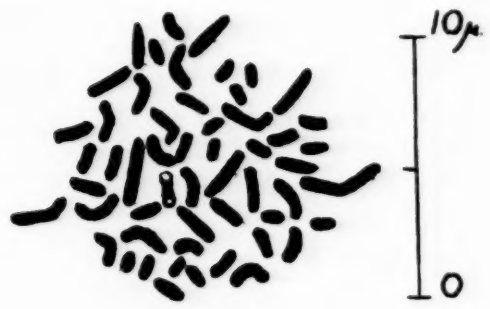


C. steveni 2n = 54

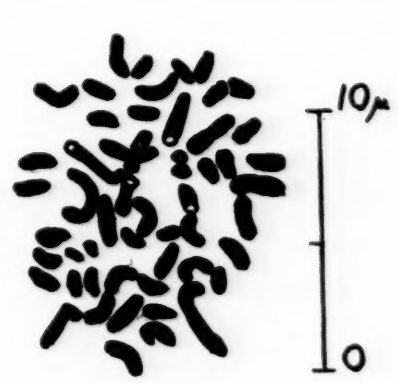
C. hierosolymitanum 2n = 18



C. hiemale 2n = 54



C. decaisnei 2n = 54



C. tunicatum 2n = 54

FIG. 4. Somatic metaphase plates of two species of Sect. Cupaniae (*C. steveni, C. hiemale*) and of three species of Sect. Autumnales (*C. hierosolymitanum, C. decaisnei, C. tunicatum*).

chromosome size, the karyotype of this species does not seem to differ significantly from those of the other species of the group.

The centromere of chromosome 5 of *C. ritchii* appears either as a short and broad achromatic region or as a long chromonema; in *C. schimperi* it is a short (fig. 3) or a very long achromatic band (fig. 5); in *C. tuviae* it is a long chromonema. The differences in the respective appearance of this centromere could not be accounted for by differences in treatment.

No satellites were found. The general size range is distinctly higher than in other *Colchicum* groups.

Sect. Cupaniae Stef.

Two species were studied: *C. steveni* and *C. hiemale*. *C. steveni* is common

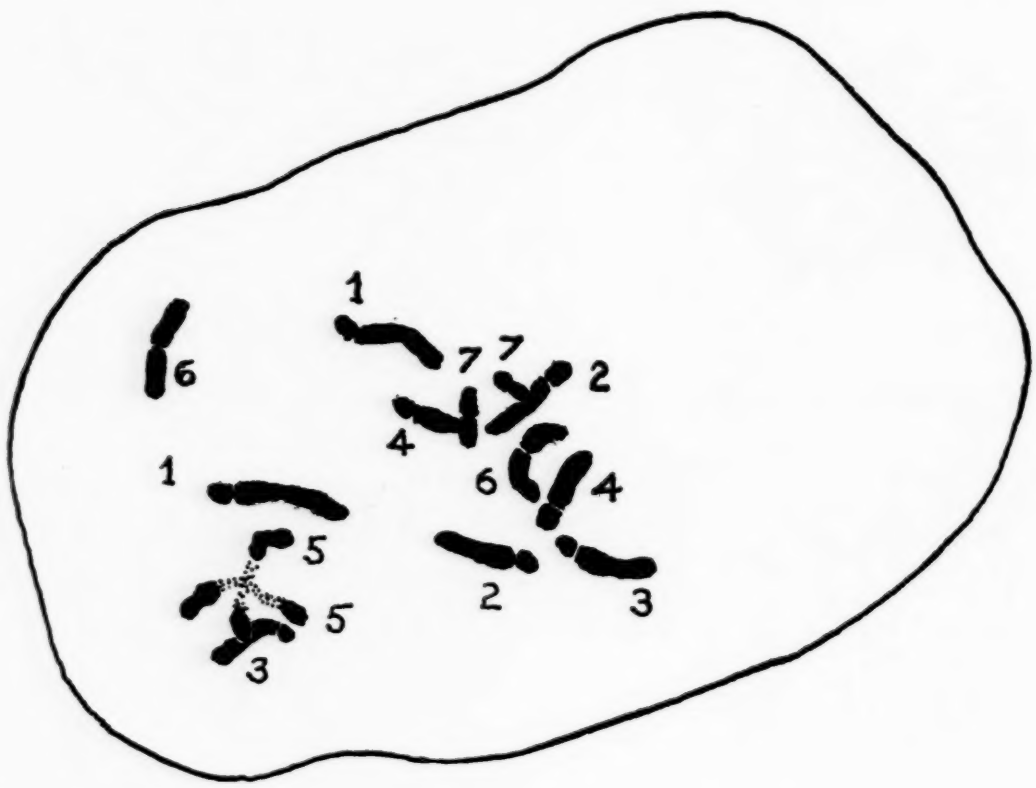


FIG. 5. Somatic metaphase plate of *C. schimperi*. Note the long centromere region in the chromosome 5 pair.

throughout the Mediterranean territories of Palestine, especially in the Batha (dwarf-shrub) associations. Its area is East-Mediterranean (see map a, fig. 1). *C. hiemale* was collected near Nicosia, Cyprus. It is endemic to Cyprus and differs from *C. steveni* in having brown anthers and fewer leaves. It may be remarked here that the number of leaves is highly significant in this genus (see Feinbrun, 1953).

The chromosome number of *C. steveni* is 2n = 54. In *C. hiemale* an exact count was made of only 53 chromosomes, but until the number can be checked on further material, it may be presumed to be 2n = 54.

The mitotic plates (fig. 4) resemble those of *C. decaisnei* and *C. tunicatum* studied by me, and of the various species drawn by Levan (1940). There are several larger chromosomes, but the size diminishes gradually to that of the smaller chromosomes which are the majority.

Sect. Autumnales Stef.

Of this section, which is characterized by the appearance of leaves after the end of flowering, three Palestinian species were investigated: *C. hierosolymitanum, C. decaisnei* and *C. tunicatum. C. hierosolymitanum* is common in olive groves and vineyards in terra-rossa soil of the hills; it has large flowers and 5–9 strap-shaped leaves. *C. decaisnei* grows in humus soil under the shrubs of maquis in N. Palestine (Upper Galilee) where annual precipitation is from 700 mm to above 1,000 mm, as well as in Lebanon and Asia Minor. The plant possesses 3–4 (rarely 5) lanceolate, usually broad, leaves. *C. tunicatum* is a desert plant of S. Palestine (Central Negev, Moav and Edom), where annual precipitation is only 150–200 mm. Its flowers are much smaller and its leaves are narrow and 5–9 in number (for distribution see map c, fig. 1).

The chromosome number of *C. hiero-*

solymitanum is 2n = 18, that of the other two species of this group 2n = 54 (fig. 4).

2n = 18 is the lowest number so far recorded for Sect. Autumnales, though the majority of *Colchicum* species studied by various authors belong to this section. *C. hierosolymitanum* is obviously a diploid species and x = 9 can be stated as the second basic number for *Colchicum*.

Unfortunately, the morphology of the chromosomes could not be analyzed in this group. The chromosomes of *C. hierosolymitanum* are unequal in length and some of them are metacentric. On the whole they are markedly larger than the chromosomes of *C. decaisnei* and *C. tunicatum*. The mitotic plates of the latter two species resemble those of *C. steveni*. No satellites have been observed.

Revision of the Chromosome List of Colchicum

Levan (1940) reports chromosome counts in ten species, nine of which belong to Sect. Autumnales. The material for his study was supplied to Levan by the Botanic Gardens of Lund and Copenhagen, and the origin of the plants studied remains unknown. Moreover, their identity is uncertain. Some of the names recorded are given by the best authorities in Colchicum taxonomy as synonyms of other species. In the following Levan's list is given with corresponding amendments.

C. montanum L. was the tenth species investigated by Levan (2n = 54), who marked its identification as doubtful. The valid name of *C. montanum* L. is *Merendera montana* (L.) Lange. The latter species studied by Fernandes (1950) under *M. bulbocodium* Ram. possesses 2n = 60.

Satô (1942) recorded chromosome numbers for three species: *C. sibthorpii* 2n = 36, *C. variegatum* 2n = 44, *C. fimbriatum* 2n = 36. While the count for *C. variegatum* tallies with that by Levan, there is a discrepancy as to *C. sibthorpii* which is given as 2n = 54 by Levan (under *C. latifolium*). Unfortunately, the origin of the plants is not known in both cases. Concerning the source of his material of Liliaceae in general, Satô says (p. 59): "Almost all the material used was obtained from pot plants most of

List of Chromosome counts by Levan	*Comments*
1. *C. bivonae* Guss. 2n = 36	Identity of the plant doubted by D'Amato (1956) who counted 2n = 52 in *C. bivonae*.
2. *C. autumnale* L. 2n = 38	Confirmed by D'Amato, and others.
3. *C. neapolitanum* Ten. 2n = 38	Identity doubted by D'Amato (1955) who counted 2n = 140 in *C. neapolitanum*.
4. *C. speciosum* Stef. 2n = 38 5. *C. giganteum* hort. 2n = 40 6. *C. bornmülleri* Freyn 2n = 42	All belong to *C. speciosum* according to Stefanoff (1926) and Bowles (1952), some being garden forms. The chromosome number for *C. speciosum* should thus be given as 2n = 38, 40, 42.
7. *C. byzantinum* Ten. 2n = 40	The name is synonymous with *C. tenorei* Parl. which is regarded as *C. neapolitanum* by D'Amato. However, *C. byzantinum* Ker. is a garden plant of unknown origin, allied to *C. cilicicum* Dammer.
8. *C. variegatum* L. 2n = 44	Newton (see Tischler, 1931) found n = 21 for *C. parkinsonii* whose valid name is *C. variegatum* L. This species thus has 2n = 42, 44.
9. *C. latifolium* S. et S. 2n = 54	The valid name is *C. sibthorpii* Bak. (Bowles, 1952). Satô (1942) recorded 2n = 36 for *C. sibthorpii*.

TABLE 2. *List of* Colchicum *species with known chromosome numbers*

Subgenus *Archicolchicum* Stef.		Subgenus *Eucolchicum* Stef.	
Sect. I. Bulbocodiae	2n	Sect. IV. Autumnales	2n
1. *C. schimperi* Janka	14 F	10. *C. alpinum* Lam. et DC.	54 DA
2. *C. ritchii* R. Br.	14 F	11. *C. arenarium* W. K.	38 DA
3. *C. tuviae* Feinbr.	14 F	12. *C. hierosolymitanum* Feinbr.	18 F
4. *C. guessfeldtianum* Asch. et Schw.	14 F	13. *C. decaisnei* Boiss.	54 F
5. *C. ancyrense* B. L. Burtt (*C. biebersteinii* Rouy)	20, 21 DA	14. *C. tunicatum* Feinbr.	54 F
Sect. II. Cupaniae		15. *C. sibthorpii* Bak.	36 S, 54 L
6. *C. cupani* Guss.	54 DA	16. *C. speciosum* Stev.	38, 40, 42 L
7. *C. hiemale* Freyn	54 F	17. *C. autumnale* L.	38 L
8. *C. steveni* Kth.	54 F	18. *C. variegatum* L.	42 N, 44 L, S
Sect. III. Luteae		19. *C. bivonae* Guss.	36 L, 52 DA
9. *C. luteum* Bak.	38 M	20. *C. lusitanum* Brot.	102 C, 106 DA
		21. *C. neapolitanum* Ten.	38 L, 140 DA

C—Castro, DA—D'Amato, F—Feinbrun, L—Levan, M—Mehra and Khoshoo, N—Newton, S—Satô.

which were raised from seeds imported by the Koicikawa Botanic Garden of the Tokyo Imperial University. For the species names, the label names on the seed bags imported were adopted in most cases." It would be interesting to find out whether the true *C. sibthorpii* comprises two chromosomal types with 2n = 36 and 2n = 54 in its natural habitats.

The *C. fimbriatum* recorded by Satô is an enigma. I have not succeeded in finding a *Colchicum* species under this name in any of the relevant literature.

Owing to numerous changes in the nomenclature of plants whose chromosome counts were published so far, a revised list is given in table 2. In this list the plants are arranged according to their taxonomic sections as given by Stefanoff in his monograph (1926). An exception is made with Section Arenariae, which in my opinion is to be included with Sect. Autumnales. The species *C. arenarium* and *C. alpinum* of Stefanoff's Sect. Arenariae do not differ from other species of Sect. Autumnales in their main characteristics, such as hysteranthous habit and especially in the surface of their pericarp, which is a very good taxonomic criterion for Sect. Autumnales (see Feinbrun 1953).

The number of *Colchicum* species with known chromosome numbers is thus 21, which is about 33% of the whole genus. From the above table it is clear that caryologically Sect. Bulbocodiae differs from the other groups of the genus. If the caryological characteristics of this section remain unaltered by additional counts, Stefanoff's subdivision of the genus into two subgenera (*Archicolchicum* and *Eucolchicum*) will have to be changed, and Section Bulbocodiae will have to be set apart.

The frequency of various chromosome numbers of Sections Cupaniae, Luteae and Autumnales, which can all be connected with x = 9, is represented in figure 6. Though based on 16 species (and 18 counts) only, the histogram brings out the relatively high frequency of 2n = 38 and especially of 2n = 54 as compared with other numbers. Although further data may modify this frequency histogram to a certain degree, it is not likely that its general trend will be changed.

CHROMOSOME GEOGRAPHY IN COLCHICUM

To gain a better understanding of the evolution within a genus, an examination

of the distribution areas of each species is most useful. The two maps of Stefanoff's monograph (1926) are obscured by the inclusion into *Colchicum* of *Merendera* and *Bulbocodium*. Besides, more recent taxonomic studies (Feinbrun, 1953; Burtt, 1951, 1956; D'Amato, 1955, 1957) have added to or wrought changes in the data concerning the geographical distribution of *Colchicum* species.

Revised maps were therefore drawn for the present paper (maps a–c, fig. 1). For sake of clarity the distribution areas of species with known chromosome numbers are marked by broken lines, whereas the remaining distribution areas are shown by dotted lines. From map 1a it is evident that Section Bulbocodiae has its main diversity in Irano-Turanian and Saharo-Sindian territories (for delimitation of the mentioned phytogeographical regions see Eig 1932–3), and a rather restricted representation in typical Mediterranean countries. All four species of Sect. Bulbocodiae studied by the author ($2n = 14$) are concentrated in the southeastern part of the area of the section (areas 9–12). *C. ancyrense* Burtt (= *C. biebersteinii* Rouy) with $2n = 20$ and 21 counted by D'Amato occurs in the central northern part of the area. Further studies will reveal the part played by each of the two basic number types ($x = 7$, $x = 10$) in the main diversity center of Sect. Bulbocodiae, i.e. Asia Minor, Syria and Iraq.

Map 1b shows the distribution of Sect. Cupaniae and Sect. Luteae. The former section is typically Mediterranean with more diversity in the Eastern than in the Western Mediterranean. All three species of this section known caryologically are hexaploid with $x = 9$. Sect. Luteae which comprises two species occupies the extreme east of the area of *Colchicum*. The chromosome number of *C. lutea* is $2n = 38$, which is a number occurring in Sect. Autumnales.

The distribution areas of Sect. Au*tumnales,* the largest section of the genus and occupying almost its whole range, appear on map c, figure 1. The main diversity center of this section is in the Mediterranean region, but a considerable number of species occur also in the Irano-Turanian region, while others are found in the temperate parts of the Euro-Siberian region.

Chromosome numbers have been counted for 12 species of this section out of 28. It is surprising that *C. hierosolymitanum,* the only diploid found so far, with $2n = 18$, is a segetal species which occupies a narrow region in the East-Mediterranean, in the southern corner of the Colchicum area. The chromosome numbers 36 and 44 were found in Greece, the Aegean coasts and in S. Italy, and some of these data need further confirmation (see table 2). The number $2n = 38$, counted in *C. autumnale, C. arenarium* and *C. speciosum,* is widely spread over the area of the genus expanding farthest in the north and reaching as far east as Transcaucasia and Persia. The hexaploids of the section with $2n = 54$ are found in the Alps (*C. alpinum*) in Greece (*C. sibthorpii*) and the East Mediterranean (*C. decaisnei*) and reach an ecological and geographical extreme with the desert species *C. tunicatum* (Negev and Edom). Thus geographically and ecologically the hexaploids cover an extremely wide range. The two higher polyploids, *C. lusitanum* ($2n = 106$) and *C. neapolitanum* ($2n = 140$), are found in the Western Mediterranean.

Speculations as to whether *C. hierosolymitanum* is the relic of a group of East Mediterranean diploid species which gave rise to the various polyploids of Sect. Autumnales are premature at this stage.

Discussion

Chromosome numbers of a genus supply valuable information as to the pattern of its chromosome evolution. What is there to be learned, then, from a study of the known chromosome numbers in the genus *Colchicum* and which interpretations, direct or indirect, of these chromo-

some numbers are to be found in previous literature?

Darlington and J. Ammal in the Chromosome Atlas (1945) give data of 10 species of *Colchicum* with the numbers 2n = 36, 38, 40, 42, 44, 54. No one of these numbers shows a preponderance in frequency over the other numbers. The basic numbers cited are x = 18, 19, 20, 21, 22, 27. The impression gained from these data is that the species of *Colchicum* form an aneuploid series. In the second edition of the Atlas (Darlington and Wylie 1955) numbers for 20 species are given. They include among others unpublished data concerning species with the numbers 2n = 14 and 2n = 18, which were communicated by the present author to Professor Darlington. Another new number included comes from Castro (1950) who found n = 51 in *C. lusitanum*. Thus, the list of chromosome numbers of *Colchicum* in the Atlas has become: 2n = 14, 18, 36, 38, 40, 42, 44, 54, 102. The basic numbers cited by Darlington and Wylie are: x_1 = 7, 9, 10. x_2 = 17, 19.

These basic numbers apparently imply the following interpretation. While 2n = 14 and 2n = 18 are diploids, 2n = 36 and 2n = 54 are tetraploids and hexaploids respectively, with a basic number of x = 9. The basic number x_1 = 10 on the other hand seems to have been derived from 2n = 40, which has to be regarded as tetraploid. 2n = 38 is a dibasic polyploid with x_2 = 19, involving the summation of the primary basic numbers 9 and 10. 2n = 102 of *C. lusitanum* is a dibasic polyploid (hexaploid) with x_2 = 17 and derive from the primary basic 7 and 10. This apparent interpretation of Darlington and Wylie can therefore be summarized by stating that numbers in Colchicum comprise diploids and polyploids, some of them dibasic polyploids.

Dibasic polyploidy is also suggested by D'Amato (1956) in his summarizing account on the cytotaxonomy of *Colchicum*. D'Amato gives chromosome numbers for 18 *Colchicum* species, comprising several unpublished counts by D'Amato and by myself. D'Amato's counts in several Italian species, verified by him on numerous populations, do not tally with previous counts made by Levan and Castro. The number for *C. ritchii* is unfortunately cited mistakenly as being 2n = 16 instead of 2n = 14. The list compiled by D'Amato comprises the following numbers: 2n = 16, 18, 20, 20 + 1 supern., 36, 38, 40, 42, 44, 52, 54, 106, 140.

The interpretation of these numbers by D'Amato (1956) (in English translation) is:

> "The discovery of Colchicum species with low chromosome numbers such as 16, 18, 20, permits for the first time to trace in x = 8, 9, 10 the basic, or some of the basic, chromosome numbers of the genus *Colchicum*. It seems very probable that starting with initial species with low chromosome numbers, a process of new species formation has developed through allopolyploidy, that is through the mechanism of doubling of chromosomes in natural interspecific hybrids (synthesis of species). A glance at the table shows that an active mechanism of speciation within the genus *Colchicum* must have been the synthesis of species, since it is evident that the chromosome number of certain species is exactly the sum of other two chromosome numbers present in the genus (for example, 36 = 16 + 20; 52 = 16 + 36; 54= 16 + 38 or 18 + 36; 106 = 52 + 54)."

It is not clear why D'Amato did not include in his considerations polyploidization by crosses of species with equal chromosome numbers. As long as monobasic polyploidy can explain at least some of the facts it seems unnecessary to introduce dibasic polyploidy. Besides, the substitution of 14 for 16 changes the possibility of some of the above number combinations.

Table 2 shows that the basic chromosome numbers 7 and 10 have been found so far in Section Bulbocodiae only. This section differs from other sections of the genus, especially from Sect. Autumnales in various important characteristics, such as synanthous habit, punctiform stigma and the surface of the pericarp (Feinbrun, 1953). It is unlikely that polyploid species of Sect. Autumnales have had a Bulbocodiae parent. D'Amato himself reports an unsuccessful attempt of crossing *C.*

ritchii (2n = 14) of Sect. Bulbocodiae with *C. hierosolymitanum* (2n = 18) of Sect. Autumnales. Though this is no final proof as to the incrossability between species from these two sections, this result does certainly not support an assumption of dibasic polyploidy in *Colchicum*. The main difficulty in the hypothesis of dibasic polyploidy in this case is its complete disregard of the fact that the different basic numbers are found in different sections.

On the basis of the evidence available, a pattern of chromosome evolution within *Colchicum* may now be suggested.

(1) In Section Bulbocodiae a number of diploid species with the basic numbers 7 and 10 were found. Further chromosome counts should show whether polyploidy occurs in this section.

(2) In Section Autumnales only one diploid among the 12 species studied is known so far. Its basic number is x = 9.

(3) Species with 2n = 36 and 2n = 54 of this section can be regarded as tetraploids and hexaploids with x = 9, though it has not been possible at this stage to identify cytologically the single genomes of the diploid (*C. hierosolymitanum*) in the polyploids. Chromosomes of these polyploids are considerably smaller, and the recognition of definite chromosome types in their metaphase plates is difficult. It is known (Darlington, 1956; Stebbins, 1950) that a reduction in chromosome size is found in some polyploid species, when compared with the respective diploid ones. Thus, section Autumnales, like many other groups of Angiospermae, includes both diploid and polyploid species. The polyploids are presumably allopolyploids. Figures of Metaphase I, scant as they are in literature on the subject, show regular bivalents.

(4) Apparently the three species of Section Cupaniae, all with 2n = 54, are also hexaploid. Their somatic metaphase plates resemble those of hexaploids from Sect. Autumnales. The basic number

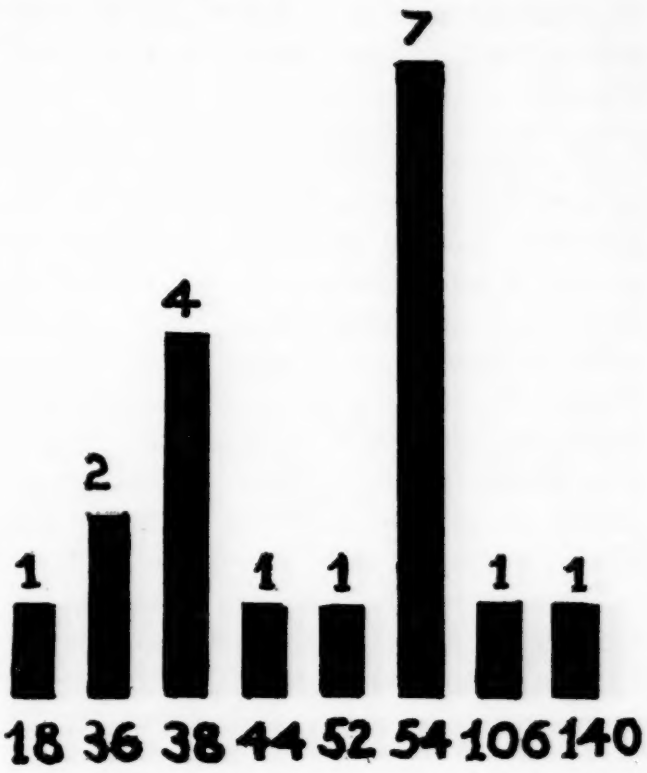


FIG. 6. Frequency histogram showing the number of species for each chromosome number group in the Autumnales, Cupaniae and Luteae sections.

x = 9 is assumed for the time being also for this section.

(5) The rather frequent occurrence and wide geographical distribution of species with 2n = 38 in Sect. Autumnales and Sect. Luteae is remarkable and requires special consideration.

a. As seen from figure 6, the hexaploids with 2n = 54 are strikingly more numerous than the tetraploids with 2n = 36, their ratio being 7 : 2. Moreover, for the two tetraploid species, *C. sibthorpii* and *C. bivonae,* 2n = 54 and 2n = 52, respectively, had also been recorded (see table 2). It seems therefore that, with the exclusion of 2n = 38 species, the hexaploid level in *Colchicum* is more successful than the tetraploid level.

b. The four species with 2n = 38, *C. arenarium, C. speciosum, C. autumnale,* and *C. luteum,* are distributed over wide geographic ranges (see map c, fig. 1) which is evidence of their high adaptive capacities. It seems plausible that these species are hexasomic tetraploids or secondary polyploids with 4x + 2 = 38, and

that the addition of an extra chromosome pair proved of great value for their success.

Though in the diploid state the addition of a pair of chromosomes might upset the adjusted balance of genes and chromosomes of an organism, on the tetraploid level such a change is likely to occur without upsetting this balance. The additional chromosome pair might even enhance the selective value of a plant, in case this chromosome contains certain genes which in additional doses produce desirable genotypic effects.

Secondary polyploids are discussed by Darlington (1956) in connection with the change in basic numbers (p. 84): "Change in basic number is something that can be faced more light-heartedly in polyploid than in diploid species. It happens with allopolyploids in two ways. The first is where whole chromosomes are added to the complement or taken from it to give secondary polyploids with a new balance and a new basic number. Thus in *Dahlia merckii* 2 pairs of chromosomes have been added to the tetraploid number so that x, which began as 8, has become 18."

D. merckii is a single species with 2n = 36 among a group of Mexican tetraploid species with 2n = 32 (Lawrence, 1931). Darlington (1937) gives the chromosome formula of *Dahlia merckii* as 4x + 4 = 36. As to the origin of the four additional chromosomes, it is not known whether *D. merckii* owes them to a process of hybridization.

The addition of chromosome pairs of one species to the genomes of another species was effected experimentally by Gerstel (1945). Gerstel crossed an autotetraploid *Nicotiana tabacum* (2n = 96) with the diploid *N. glutinosa* (2n = 24) with the aim of transferring resistance to tobacco mosaic virus from *N. glutinosa*. After repeated backcrosses of the hybrid to the diploid *N. tabacum* some of the segregants contained 25 and 26 pairs of chromosomes instead of 24 pairs as in normal *N. tabacum*. The identification of the additional chromosome pairs as originating from *N. glutinosa* was possible, owing to the fact that only those segregants were resistant to tobacco mosaic virus. These plants were named by R. E. Clausen "alien addition races." Gerstel (1945) and Stebbins (1950) claim that no similar cases are known in natural populations. Gerstel assumes that rare crosses between normally self-fertilizing plants could "make the working of the hypothesized mechanism possible," but in his opinion this mechanism can hardly explain the origin of aneuploids in cross-fertilizing plants, since "only isolation could prevent their reverting to the parental types." It seems, however, that the survival of alien addition types endowed with better adaptive qualities than their parents, is not out of the question, especially where *perennials with occasional self-fertilization* are concerned.

In this connection mention may be made of what is known about the breeding system in *Colchicum*. Evidence in this regard is rather poor. Kirchner, Loew and Schroetter (1934) supply some information on *C. autumnale* (2n = 38). The flowers are proterogynous and are usually pollinated by various insects such as bumble bees, honey bees, hover flies and butterflies. However, self-pollination also occurs, usually at the end of anthesis and in the absence of pollinators. Nucellar embryony in *C. autumnale* was reported by Frulani. *C. alpinum* (2n = 38) is also proterogynous and is pollinated by bees. Apparently vegetative propagation occurs in many species. Zohary (1938) describes propagation through cormlets in *C. steveni*, a feature also frequently observed by the present writer. *C. tunicatum* too apparently reproduces vegetatively.

Occasional self-pollination, nucellar embryony and vegetative propagation in these geophytes could all favor multiplication of the new chromosome races and, merely by enlarging their numbers, provide them with better chances of establishment. While vegetative propagation

by corms and cormlets might have a limited dispersal potential, nucellar embryony resulting in seed production could provide the plants with a normal dispersal range.

(5) Mitotic non-disjunction in plants mainly propagated vegetatively could explain the occurrence of 2n = 38, 40, 42 in *C. speciosum,* which is one of the Colchicum species grown for ornament and distributed in several varieties by nurseries under various names. The same may be true for *C. variegatum.* In root tips of *C. autumnale* Levan (1940) occasionally found 39 and 40 somatic chromosomes along with 38.

(6) The two West-Mediterranean species with very high chromosome numbers, *C. lusitanum* with 2n = 106, and *C. neapolitanum* with 2n = 140, may be regarded as high polyploids of x = 9, with a few chromosomes lost. Thus, *C. lusitanum* can be regarded as (12x − 2) = 106, and *C. neapolitanum* as (16x − 4) =140. It is improbable that at such high polyploid levels the loss of a few chromosomes would have an adverse effect on the plants in question.

On the basis of evidence available, as well as on the considerations brought forward here, the following conclusions may be made as to the main lines of chromosome evolution in *Colchicum.*

At the diploid level chromosome evolution in *Colchicum* involved fundamental changes in basic chromosome numbers connected with the differentiation of main groups or sections of the genus. At the present state of our knowledge of chromosome numbers in *Colchicum* it is premature to attempt any guess as to the direction of these changes, i.e. increase or decrease of the basic chromosome numbers.

Allopolyploidy played a decisive part in speciation within Sect. Autumnales and presumably in Sect. Cupaniae. The hexaploid level apparently presented certain advantages for the establishment and expansion of species over other polyploid levels.

Superimposed on polyploidy, another process has been of major importance in the evolution of some groups of *Colchicum* (Sect. Autumnales, Sect. Luteae), namely, the addition of single chromosome pairs to the genomes of tetraploids, as well as the loss of single chromosome pairs at higher polyploid levels, such as 6x, 12x, 16x.

The species with 2n = 38 may be regarded as hexasomic tetraploids. The possibility of their being "alien addition types" of R. E. Clausen seems not improbable.

Summary

(1) Chromosomes of nine *Colchicum* species from East-Mediterranean countries were studied (table 1). Low chromosome numbers, 2n = 14 and 2n = 18, were found in *Colchicum* for the first time, thus establishing the basic numbers x = 7 and x = 9 in this genus. Idiograms of four species belonging to Sect. Bulbocodiae could be drawn (fig. 3). The chromosomes of these species are prominent by their large size.

(2) The nomenclature of *Colchicum* species whose chromosomes were counted by various investigators is revised. It emerges that some of the variability in chromosome numbers in *Colchicum* is intraspecific. In table 2 a revised list of chromosome numbers in *Colchicum* is given.

(3) When species with known chromosome numbers are arranged in their taxonomic sections, it becomes clear that variability in chromosome numbers is unevenly distributed within the genus. Sect. Bulbocodiae comprises only diploid species with 2n = 14 and 20 and with basic numbers x = 7, 10. Sect. Autumnales comprises one diploid species with 2n = 18 and the basic number x = 9, and various species with the chromosome numbers 36, 38–42, 42–44, 52, 54, 106, 140. Three species of Sect. Cupaniae have 2n = 54 and one species of Sect. Luteae 2n = 38.

(4) New maps of the geographical distribution of *Colchicum* species show the

diversity center of each section. Areas of species with known chromosome numbers are specially marked.

(5) The pattern of chromosome evolution in *Colchicum* is discussed. It is concluded that allopolyploidy and secondary polyploidy, involving addition or loss of single chromosome pairs, played a major part in speciation within *Colchicum*.

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ON POPULATION STRUCTURE IN GENERALIZED HUNTING AND COLLECTING POPULATIONS [1]

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INTRODUCTION

For the purposes of this research generalized hunting and collecting populations may be defined as those peoples dependent for sustenance on a wide variety of foods obtained by hunting and collecting methods in patterns which change seasonally, and among whom food storage and preservation are of little or no consequence. They have no domestic plants, nor any domesticated animals other than the dog, which is primarily utilized as an adjunct to hunting and not as a direct food source. More than a dozen regional clusters of peoples at this simple economic level existed at the time of historical contact. The Australians and the Tasmanians in Australasia are well known examples. Negritic peoples in eastern Asia at this level include the Aeta of the Philippines, the Semang of the Malay Peninsula, and the inhabitants of the Andaman Islands. In Africa all of the so-called Bushmen tribes and the rain forest Negritoes of the Congo Basin are in this economic group. A small group of jungle tribes in India falls into this category. In the New World the Shoshoni tribes of the Great Basin belong here, despite the relative importance of the piñon nut in their economy and the ease with which it lends itself to preservation during winter months. It is probable that the inland Athabascan and Algonquin speaking peoples of Canada belong with the others in spite of assistance provided by the climate for the preservation of meat products through the winter months. The same factors suggest the possible inclusion of the Caribou Eskimo. In South America the Ona of Tierra del Fuego and the adjacent coastal and more northerly plains tribes belong in this classification.

Several groups of peoples technically classed at the hunting and collecting level of economy must be explicitly excluded. The basis for exclusion generally rests upon their access at least seasonally to rich and abundant food resources of limited variety combined with more effective methods of preservation, so that survival is less upon a day-to-day basis and some accumulation of wealth is possible. These richer sources of energy influence density, population structure, and social and political organization in such a way that the generalizations derived from the more stringent economies no longer apply. The acorn gathering Indians in California are excluded since the abundance of this primary source of food and its easy preservation renders them more analogous in density to the primitive horticultural peoples of the world. The tribes in the Northwest coast area, for whom salmon provided the primary food source, are likewise omitted from consideration. The horse nomads of the Great Plains may, during the worst seasons of the year, approximate our generalized conditions, but during the buffalo hunting season their culture took on more complex aspects and for this reason they will be disregarded. The coastal Eskimo perhaps present a borderline case, but since during the critical winter months their survival depended upon hunting of a limited variety of sea mammals they do not seem generalized

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enough in their economy for inclusion here.

The bearers of these simple generalized hunting and collecting economies include representatives, at least in hybridized form, of all the major racial groups. They live through the near maximum range of earthly environments with mean annual rainfall ranging from a minimum of 4 inches to values in excess of 200 inches; and in temperatures that range from desert tropics, through tropical rain forests, to temperate zone and probably into the continental Arctic. Culturally, their typologies range from the paleolithic of the Tasmanians, through epipaleolithic forms, into those which include contributions from obviously neolithic sources. At this economic level, with its simple day-to-day pursuit of food, there are certain broad similarities among all the peoples who belong to it. A number of these are well recognized in the existing anthropological literature. Such peoples are characterized by having little or no accumulated wealth, they lack class differentiation, they are united by no effective political authority, and organized warfare is lacking. Their densities in the best cases seldom range above 1 to 2 persons per square mile and in the worst environments 100 square miles may be required to support each individual.

Discussion

In addition to these readily visible generalizations, there exist others which do not rise easily to the surface of unquantified data. Ethnographers with few exceptions have systematically particularized the culture of each people. They have not only resisted the search for underlying uniformities, but have failed to ask the questions which would lead to their discovery. The generally humanistic approach which characterizes the work of most anthropologists has failed to provide the quantified data which are needed to explore relationships between variables within a single culture, or across many cultures.

The regularities to be explored in the remaining sections of this paper cluster about three themes: (A) territoriality; (B) population dynamics; (C) cultural cohesion. These formulations are to be considered preliminary in nature since the quantified data upon which they depend are extraordinarily rare in the literature and opportunity has not yet allowed comprehensive search of all pertinent publications. Enough sources have been covered to indicate the general range of phenomena, but detailed documentation must await time for further elaboration. These generalizations are not offered in a dogmatic spirit. It is to be expected that exceptions to them will occasionally occur among the peoples under consideration. But it is believed that they have a high probability of becoming uniting principles for the analysis of this level of economy.

(A) Territoriality

Like most terrestial vertebrates, man at generalized hunting and collecting levels of economy shows clear-cut territoriality. It is expressed in hunting and collecting rights in a given area and not of possession of realty. In most groups it is vested in the local band, or horde, and boundaries are commonly defined by natural topographic features. In flat, arid areas boundaries may be functionally defined in terms of waterless stretches. The widespread occurrence of territoriality among humans, as well as among infrahuman groups of terrestial vertebrates, seems to be a consequence of the need to insure that for species survival the best breeding areas of a range should not be overpopulated. Among a few generalized hunting and collecting peoples, such as the Shoshoni, territoriality in the conventional sense does not seem to exist (Steward, 1938). But since this same group of tribes in an over-all sense show that population density is rather rigorously determined by environmental variables (as indicated below), it must be assumed that some informal and amorphous

system controls population numbers without rigidly defined territories being involved. Even the best of ethnographers, and Steward is certainly among these, provide little data for the solution of such questions, since they are not customarily emphasized.

Anthropologists for a number of decades have tacitly maintained that human populations are free from all forms of environmental determinism. The sweep of this assertion, which resulted as a reaction to earlier claims that many aspects of culture were determined by the environment, has obscured the fact that at the simple levels of generalized hunting and collecting economies population densities may be primarily determined by environmental factors. This is not to deny that at any human level population densities are also subject to the influence of cultural variables, but these factors may be less important than those inherent in the environment in the determination of densities considered here. The first evidence for the rigorous environmental determination of human density was presented (Birdsell, 1953) for the Australian aborigines. In that arid continent it was found that mean annual rainfall taken alone constituted the most important environmental determinant of native densities and that the curvilinear coefficient of correlation, $r = .8$. Rainfall for these tribal groups ranged from 5 to 151 inches for annual average, and its relationship to tribal area with an inverse logarithmic function. This relationship was based upon 123 tribal groups which were considered ecologically homogeneous in nature. It seems clear that if other effective environmental variables had been introduced into the analysis at that time, the coefficient of correlation would have been even higher.

In a recent but as yet unpublished study, Vorapich has taken Steward's data for the Great Basin Shoshoni and demonstrated a similar environmental determination of human densities in that area. Her coefficient of correlations approximates .5 for a much smaller series of tribes. As in the earlier Australian analysis a single environmental variable, mean annual rainfall, was utilized in the analysis. Since the Shoshoni show a much narrower range in this variable, from 4 to 14 inches annually, it will be seen that her sample covers only a small sector of the comparable Australian data. By reanalyzing that portion of the Australian sample covering the same limited rainfall range she has shown that her coefficient of correlation falls but little below that for a comparable sector of the Australian data. It would seem that the Shoshoni materials reveal a lower correlation coefficient primarily as a result of the more limited range of the primary variable. It may be concluded that the Shoshoni are as rigorously determined in their population densities as are the Australian aborigines.

This parallel is the more remarkable in the light of the contrast in the economies. The Shoshoni subsist almost entirely upon plant products and make large use of the piñon nut harvest, a product which is easily stored and upon which they are dependent for their winter sustenance. The Australians are to a much greater degree hunters and have little or no food preservation. The contrast between the two groups is further heightened by differences in topography. Most Australian bands live in country of relatively low relief and the altitudinal effects of changing flora and fauna are generally absent. On the other hand, the Shoshoni families customarily range from the desert floor at the proper season of the year, to the high altitudes of the numerous mountain ranges which cross the Great Basin and which provide the piñon nut harvest upon which they are so dependent. The Shoshoni show considerably higher densities for a given value of rainfall than do the Australians. Since the general levels of technology are similar it must be assumed that these altitudinal variations allow the greater population density found among the Shoshoni.

These two analyses of the environ-

mental determinants of human densities at generalized level of hunting and collecting populations are the by-products of meticulous field work by two individual investigators. The Australian data are based upon the extraordinarily detailed tribal maps for that continent published by Tindale (1940), whereas Vorapich's treatment rests upon the very able field work of Steward (1938). It may be classed as one of the professional misfortunes of anthropology that few other field workers have realized the great potential of such detailed studies of population distributions, so comparative studies for other groups may not be possible now or in the future. But the qualitative descriptions in the literature strongly suggest that other populations at comparable levels of culture show densities also primarily determined by environmental variables. It should be noted with some caution that whereas these two groups, living in arid regions, show a high correlation with a single environmental variable, and this in both cases, mean annual rainfall, that in other climates and places a multivariant analysis of the environmental factors conditioning density would undoubtedly be necessary. The equation which relates primitive human densities to their environment does not allow projection from one region to another. For each local group of populations the fuller array of environmental determinants must be analyzed. The local flora and fauna available to the human populations will vary according to the phylogenetic history in that region. Finally, the ability of each human group to utilize these sources of energy will vary with their extractive efficiency as determined by their technology.

The working assumption based upon the two previous examples that generalized hunting and collecting populations show densities primarily determined by environmental factors clearly implies that such populations are in stable equilibrium with the carrying capacity of their country. Equilibrium as used here allows for minor oscillations in time but implies that corrective forces exist which tend to return densities to their proper values in terms of available resources. Such corrective forces may be inherent in the dynamics of the population, in the environment itself, as in times of drought or failure of food resources for any other reason, or they may involve cultural factors which operate so as to help maintain an essentially stable population.

(B) Population Dynamics

One of the basic parameters in any evaluation of the role of population dynamics of a people involves the estimation of the intrinsic rate of increase, the rate of increase in an unlimited environment. While this may be determined with some facility in experimental populations of animals, man seldom provides such a situation. In a recent analysis it has been shown (Birdsell, in press) that four recorded instances in human history give some basis for making an estimation. Three of these examples occurred in the insular environments of Tristan da Cunha in the South Atlantic, Pitcairn Island in the eastern Central Pacific, and Cape Barren Island in Bass Strait between the mainland of Australia and Tasmania. In each instance available data suggests that these simple horticultural populations follow an intrinsic rate of increase in which the population doubled in each generation. This rate continued essentially unchanged until the population reached a point at which the food resources of the environment exert a marked depressant effect. In fact, they overshoot the theoretical curve of approach to the equilibrium value. Since it may be questioned whether the data from these horticultural populations would apply to the generalized level of hunting and collecting peoples, it is fortunate that a fragmentary record remains for a similar experimental population in Australia. There, in an interesting late 19th century account, is recorded the fate of a Marawra tribesman who, accompanied by two of his wives, disappeared

into the uninhabited mallee country to the west of a frontier settlement on the Darling River. When found again thirty years after the original exodus, this little group of aborigines had increased to 28 in number. Fragmentary as the data are, they indicate that for this group the intrinsic rate of increase was closer to that of tripling the population each generation than of doubling it. It lends some assurance that the data from the other three examples do, in fact, apply to the intrinsic rate of increase of hunting and collecting people in an unlimited environment. Until better data are provided, it is safe to assume that their numbers will double with the passage of each generation.

This potential rate of increase which seems to characterize even simple human populations requires some reconciliation with the concept of stable populations as determined by environmental variables. In a broad sense, it is clear that the potential for population expansion acts as a buffer against the threat of extinction which lies inherent in the vagaries of life at this technological level in an uncontrolled environment. The forces which contain this potential rate of expansion are both environmental and cultural in nature. It is characteristic of generalized hunting and collecting peoples that proper foods for infants are lacking. Without domestic animals only mother's milk is available. In the absence of agriculture, starches of the proper type for infant feeding are scarce or absent. A direct consequence of this environmental pressure is that the weaning of infants is much delayed. Descriptive accounts generally agree that such people nurse their infants from 2 to 4 years after birth, and it may reasonably be assumed that the average duration of breast feeding is close to three years. The importance for survival of band and individual mobility combined with the hard living and variable nutrition available at these cultural levels precludes the nursing of two children simultaneously. It is not entirely surprising that, where a high infant mortality fails to balance population numbers, infanticide is generally resorted to. Quantitative data on rate of infanticide are rare but several accounts suggest that it customarily ranged to as high as 30 per cent of the births among some of the Australian aborigines. Whereas infanticide is clearly in the realm of cultural variables which tend to control population at the equilibrium level, it is based upon the rigorous requirements of the environment.

This protracted period of nursing of the human infant at generalized hunting and collecting levels of economy results in a low variance in the effective number of offspring per mating and consequently influences some of the evolutionary processes which operate on such populations. At higher cultural levels, as among pastural and agricultural people, the earlier weaning of offspring allows for their much more frequent procreation. Among the simpler populations, the scanty evidence suggests that the range of effective offspring per mating ranges from 0 to perhaps 6, whereas at higher cultural levels it may be more nearly from 0 to 12. Thus variance of the offspring per mating among the simpler economic groups effectively approaches a constant value and it may be estimated to be equal to 2, or perhaps slightly less, regardless of race and climate. This constant variance affects the size of the effective breeding populations and simplifies its calculations for such groups where primary and vital statistics are so scanty. In the equation given by Wright (1938)

$$\tilde{N} = \frac{4N - 2}{\sigma_K^2 + 2}.$$

In essence, the equation means that the effective size of the population for evolutionary processes is a direct function of the size of the breeding population and an inverse function of the variance of the effective number of offspring produced. It is here contended that for generalized hunting and collecting people the variance is essentially a constant owing to the pro-

tracted nursing period in such cultures, and hence the effective size of the population becomes directly related to the size of the breeding population alone. This regularity is of some importance in considering how random genetic drift will influence such groups for whom demographic data are exceedingly scarce.

Another influence which is commonly considered as a potential factor in the structuring of human populations is known as assortative mating. Positive assortative mating involves likes marrying likes on a phenotypic basis. Its consequence is to increase genetic homozygosity and to diminish heterozygosity. Negative assortative mating produces opposite results with an increase of heterozygosity. It has yet to be demonstrated that either of these forms of mating systems are of evolutionary significance in any human population. Among the uncomplicated populations considered here, women are universally married at an early age. The number of permanently unmarried adults in such groups is, as a rule, of the magnitude of 1 or 2 per cent. Under these circumstances, even though the detailed data are wanting, it is safe to assume that assortative mating, whether in positive or negative form, is not a factor in population structuring.

Another system of mating which may possibly influence populations is known as inbreeding. This process involves mating between biologically related individuals and in experimental populations it does have the effect of markedly increasing genetic homozygosity. As applied to natural human populations, however, the term has been much abused. In part this distortion has arisen from the fact that many anthropologists have confused classificatory kinship systems of mating with the biological systems which actually prevail in populations. Thus a fair minority of the world's people show a classificatory preference for marriage between first cousins, either cross or parallel. This social abstraction is all too frequently translated among anthropological circles into the belief that such systems involve actual marriages between biological cousins with a high degree of frequency. It will be shown elsewhere that the kinship abstraction does not have biological validity; that where quantitative data are available the frequency of such biological matings is low, that populations show no significant increase in genetic homozygosity. It may safely be concluded that generalized hunting and collecting peoples do not in a genetical sense show any significant degree of inbreeding.

(C) Factors Affecting Cultural Cohesion

Three basic social units seem to be constantly present among people at a generalized hunting and collecting economy: (1) the biological family; (2) the band; (3) the tribe. The biological family occurs in one form or another among all human groups. Among the groups under discussion it either takes the form of monogamy or goes further and allows a minority of males to practice polygamous marriage. It is frequently claimed that the human biological family is cultural invention. While it is true that it occurs in a number of forms, it is better considered as a biological prerequisite for species survival. Among hunting and collecting peoples, the economic partnership between an adult male and one or more adult females is a necessity for the successful rearing of the next generation.

The next largest basic social unit among the peoples under discussion is known as the band, horde, or local group. In the anthropological literature it is rather loosely defined either as an extended family or a group of several related families. While quantitative data are lacking for a proper analysis, it is clear that among most groups the band is larger than would be reasonably expected from among the survivors of a single extended family. Few data exist to indicate how the several families may, in fact, be biologically or socially related. Band size varies considerably among different groups

and the range may perhaps be estimated as averaging 20 to 100 individuals. Anthropologists in general have not examined the composition of the band among their respective peoples and have had little interest in the social and environmental forces which tend to produce human groups of fairly constant size which function as a basic social unit for at least a portion of the seasonal cycle.

An unusual awareness of the general problem has been shown by Steward who says (1938, p. 258), "All peoples in an area of low population density have some form of politically autonomous, landowning band, which is greater than the bilateral family. The size of the band and the extent of the territory it utilizes are determined by the number of persons who, due largely to ecological factors, habitually cooperate at least during part of the annual round of economic and social activities. Band unity is expressed in a consciousness of common interest and submission to some degree of central control during the community enterprises, although such control may be lacking during parts of the year. The authority of the leader is consequently small and temporary and its position is seldom a fixed institution." He goes on to define the two types of bands which occur among generalized hunting and collecting peoples. The commonest consists of the unilineal, exogamous, patrilineal, patrilocal band which consists of actual or fictitious relations. It occurs among peoples with an emphasis on hunting and hence is male-dominant culturally. The ecology that prevails among such peoples prevents the size of the band from ranging much outside of 50 to 100 people. It is characteristic among Australians, Tasmanians, Semang, African negritoes, northern Bushmen, Fuegians, and Southern Californians. The second type of band is known as the composite band. Since it consists of unrelated families and is not unilineal, its members need not observe band exogamy. Ecological factors allow the size of these bands to approximate 100 individuals. It is characteristic of the southern Bushmen, the Andamanese, many Canadian Algonkins, and Athabascans. Steward has indicated that theoretically a third type of band, which would be the matrilineal counterpart of the first, should exist among some primitive agriculturists, but these are outside the scope of our interest here.

Some system of equilibrium forces, involving both ecological and cultural factors, tend to maintain appropriate population size for band structure for given local conditions. Since anthropologists have not defined details of the nature of the cultural forces involved and have gathered no materials which allow a detailed examination of the ecological factors, it is impossible to construct models to explore the systems occurring among various peoples. On the other hand, it does seem clear that band size is not primarily determined by chance factors and that systematic forces do exist. One may hope that future generations of field workers may collect enough demographic and ecological data to provide a basis for such investigation.

The third basic unit, the tribe, is another loosely defined anthropological abstraction. In essence, it refers to a cluster of culturally and linguistically related groups of peoples but may range in size from a few hundred to several millions of persons. This range of variation occurs as a continuum so that arbitrary distinctions between various forms of tribes have not been defined. The factor most importantly affecting tribal size seems to be degree of centralized political authority. It is perhaps sufficient for this problem to state that tribes among generalized hunting and collecting peoples are not political entities, and that central political authority is largely or completely absent. Such tribes do show some cohesiveness but it is based upon linguistic and cultural relationships alone, as reinforced by spatial relationships. It seems to have been previously unnoted that there is a broad tendency for the aggregation of related

bands which comprise such tribes to show modal values approximating 500 individuals. This is true for the Australians (Birdsell, 1953) and the Tasmanians, both of which were characterized by patrilineal exogamous bands. It seems to also have been true of the Andamanese, with their composite band structure. Other groups may reveal a tendency toward somewhat higher values as a central statistical tendency. It would be of interest to test whether these tendencies toward a constant size of tribal population are a direct function of the size of the bands interacting as seems most likely or whether the limiting factors lie in the limitations upon interactions among a given number of individuals. In the former case, one would expect average tribal size to vary directly with the mean number of persons making up the bands. In the latter instance total tribal populations would tend to approximate a constant size regardless of band size. Unfortunately the data to make such tests do not seem to be published. In any case, the constancy of population size among the tribes under consideration imply a system of equilibrium forces. The remainder of this paper will be devoted to the tentative identification of some of these. Since empirical data are lacking, the stabilizing forces postulated will have to be explored by means of model constructs. The following models are intended to apply only to exogamous patrilineal band organization.

Social equilibrium, like mechanical equilibrium, results when a system of forces act in such a way that deviations from the normative position set up restoring forces which tend to re-establish the balanced condition existing prior to the disturbance. Such a stable condition may be obtained in the most elemental case with but two opposing forces, but it would be unrealistic to assume that the forces act so simply. It will be better to consider that an unknown number of forces are involved in the suspension system of balancing tribal numbers in these simple economic groups, even though this paper will attempt to outline in exploratory fashion only two of the more important opposing forces. It must not be assumed that a stable equilibrium involves either a single system of balance or that the restoring forces operate in a direct, uncomplicated fashion. The empirical data from Australia determining the statistical abstraction which describes the average size of tribal population approximating 500 individuals in fact represents a fairly wide range of values, and indicate that serious disturbances of the balanced condition may not be compensated for until tribal population actually falls below 200 individuals or exceeds 800 individuals. The process of restoration may well involve oscillations rather than a single direct return to an ideal balance.

One of the primary factors in the system of equilibrium involves the number of local groups or bands which cohere to form a single relative homogeneous linguistic and cultural unit, or tribe. Another and opposing force depends on distance as an isolating mechanism in cultural behavior. Both of these forces are based in a spatial geometry and it is proposed to explore some of their idealized characteristics through simple geometric models. In the exogamous patrilineal band structure characterizing most of Australia, cultural impact and change primarily operate through band contact. This is not to say that interband and intertribal contacts between families do not occur, but rather that normally they seem to be conducted by bands. At the first sight it would seem that intertribal marriages might be the mechanism of cultural diffusion in the continent of Australia, but these are universally patrilocal, since the wife joins the band of the husband. The woman's position there is such that she has little chance to influence language, ceremony, or the male functions in the total culture. These imported wives are silent nonentities until they learn the language of their husband's group, and then they are quickly absorbed into the hus-

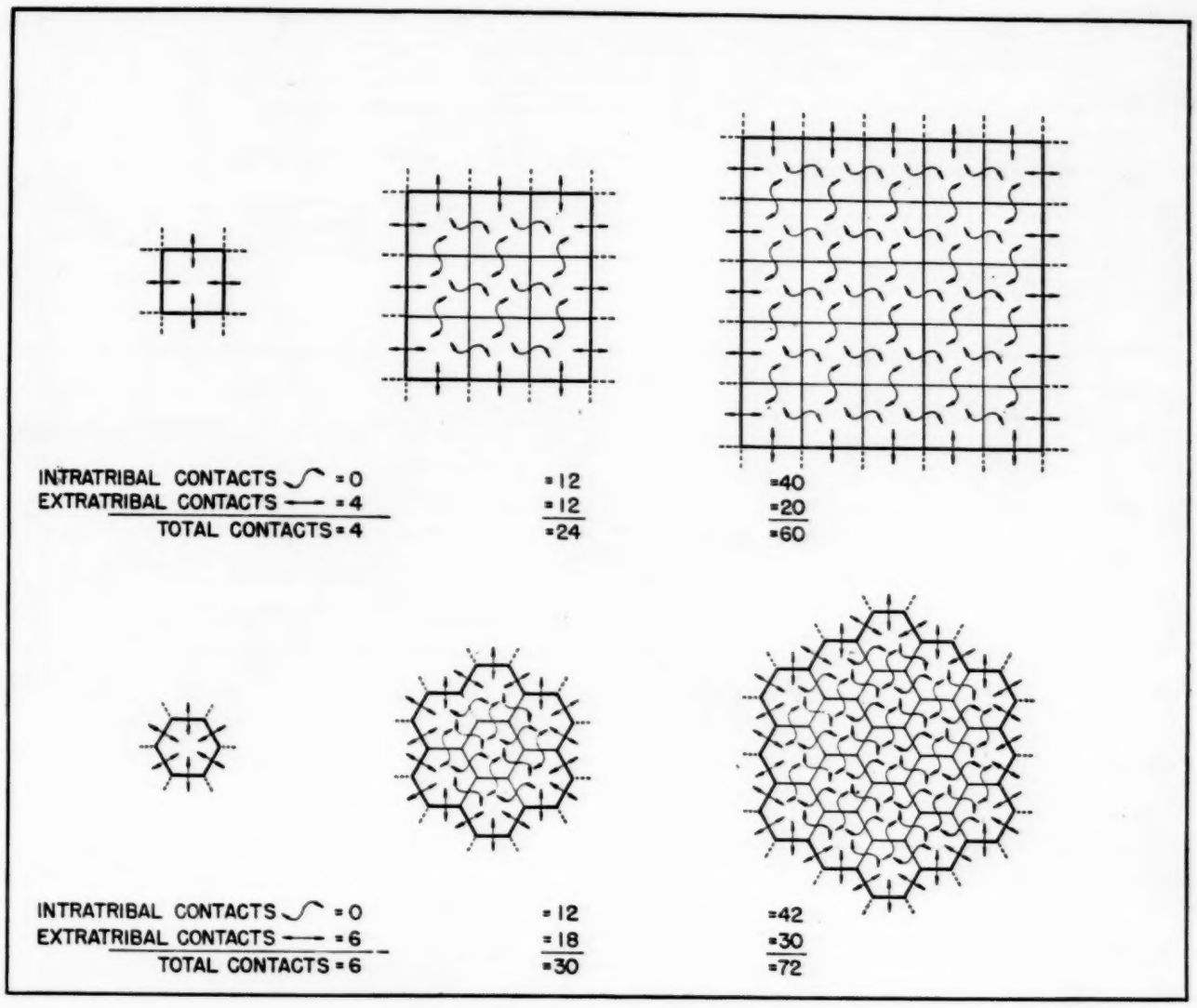

FIG. 1. Geometrical arrangements to show contacts available to local groups.

band's band and tribe. On the other hand intertribal marriages may be treated as systematic expressions of the rates and directions of intertribal and interband interactions. For it cannot be doubted that wives are obtained from groups with whom social relations are at least occasionally established. Thus rates of intertribal marriages may be taken as a secondary index expressing in indirect fashion the frequencies and directions of intertribal contacts which have never been systematically observed.

MODEL OF SPATIAL EFFECTS UPON BAND SOCIAL INTERACTIONS

In figure 1 a series of simple geometrical arrangements are shown involving two idealized assumptions concerning the number of extra-band contacts physically, that is geographically, available to each local group. The upper 3 diagrams are based upon the assumption that each band will have 4 neighboring local groups with which it has effective contacts along common boundaries, with apical contacts ignored. The lower series of 3 diagrams are based upon the assumption that each local group will have contiguous boundaries with 6 other adjacent bands. The five-sided configuration must be ignored since it cannot be graphically shown in two dimensional space. The left hand diagram in both rows represents the assumption that the single band is the unit of cultural cohesiveness and that culture will change uniformly if gradually in crossing each band boundary. The inte-

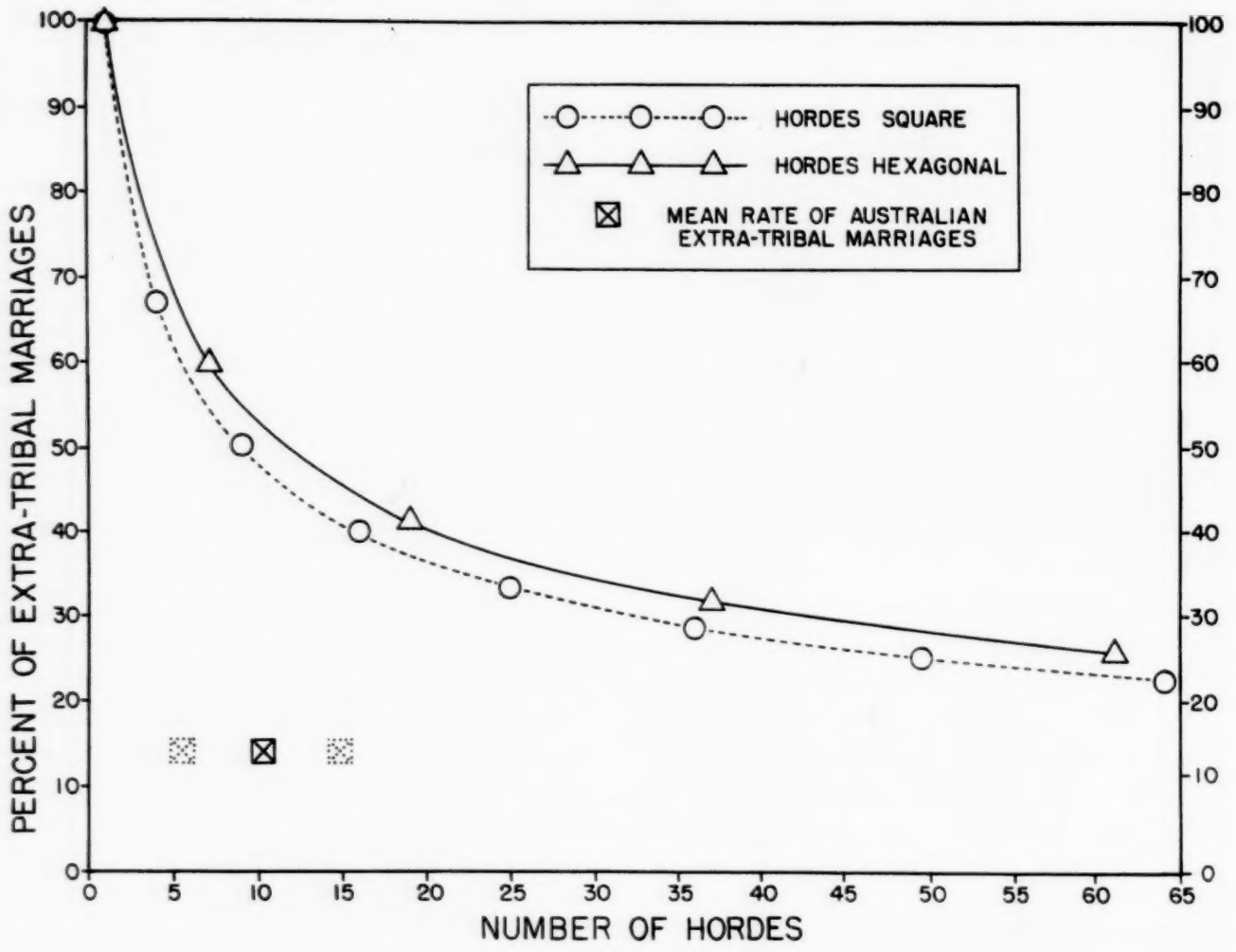

FIG. 2. Extension and summary of trend in diagrams of figure 1. For explanation see text, p. 199.

gration of Australian spatial relations in either geometry would result in a continent in which there were no tribes and for which cultural change could best be shown by a series of clines. Under such a system, with each band equivalent to the tribe and with patrilocal exogamic marriage uniformly practiced, all marriages would be intertribal in nature. If frequency of social contacts followed the pattern of intertribal marriages as it is assumed here, then the spread of cultural changes would be a slow, gradual and uniform process and aboriginal cultural space would be structured only at the band levels.

In the middle diagrams of both rows it has been assumed that on the average tribes consist of 9 bands in a four-sided space and 7 bands in a hexagonal space. Both of these concepts imply that clusters of bands are the units of cultural cohesion as in fact the evidence indicates. If it is further assumed that the rate of interband exchange of women, and of other forms of social contact, is the same on all of its boundaries, whether these involve extratribal or intratribal bands, then an important geometrical principle in the cultural relationships emerges. For the configuration involving four-sided bands the number of intertribal contacts or marriages is reduced to 50 per cent of the total, whereas for the hexagonal shaped bands the intertribal marriages are reduced to 60 per cent.

Figure 1 carries the investigation one step further in the right hand diagram, which involves 25 bands in each tribe for the square configuration and 19 bands in each tribe for the hexagonal pattern of space. Utilizing the previous assumptions it is found that increasing the number of bands per tribe has further reduced the

number of extra-tribal marriages and contacts, even though no cultural barriers have been erected at tribal boundaries. For the 25 bands with the square shape, the extratribal marriages or contacts are reduced to 33⅓ per cent of the total, and for the 19 hexagonally shaped bands the value is about 42 per cent.

The trend established by these diagrams has been carried further and summarized in figure 2. It will be seen that for both types of geometrical configurations an increase in the number of bands per tribe, which represents the culturally coherent unit, is followed by a smoothly diminishing proportion of extra-tribal marriages and presumably contacts. It will be noted that the hexagonal configuration shows a less abrupt reduction in such frequency of contact but that it follows the same general pattern of the simpler four-sided configuration. This is a version of the simple geometric principle that for similar figures the contained area increases more rapidly than does the bounding perimeter.

At this point it is of interest to empirically check the actual configuration of Australian tribes as shown by Tindale's map (1940). There are no data giving a detailed plotting of bands in a geometrical sense so that it is necessary to assume that their general form will approximate that of the tribe which contains them. Thus an essentially circular tribal area will be filled with bands which are assumed to be roughly circular in their own shape; that is, not markedly elongated in either major axis. On the other hand, a tribal territory which is narrow and long must be assumed to contain bands with somewhat similar shapes. This assumption cannot be tested and it may well err in the direction of systematically giving a larger number of sides per band than in fact exists. This possible error, however, is in part corrected for by ignoring in the count those contacts which represent the apices of tribes in contact. In practice the bands in these apical territories certainly would have contact despite the narrowing geometry of the tribal boundaries. So that perhaps it can be considered for the present that these two factors tend to compensate for each other.

Certain other points must be considered. For example, if the sizes of tribal areas are changing unduly rapidly, as may occur under abrupt changes in ecology, as going from a desert to a riverine area, then the count will be distorted. In a similar fashion coastal tribes will yield too low a count in contact boundaries. For these reasons the basic series of tribes published earlier (Birdsell, 1953) have been utilized in the count, and 100 tribes from these data have been examined for the number of contacts along their boundaries. The results indicate an average of 5.5 tribal contacts for each of the 100 tribes. The results strongly suggest that the hexagonal configurations in figure 1 more closely approximate empirical conditions in Australia (and not unlikely elsewhere) than does the simpler square configuration.

Since the curves show that the geometrically determined number of extra-tribal marriages or contacts are a function of the number of bands per tribe, it is of some importance to try to estimate for Australia the average number of local groups per tribe. A tabulation of the band count for a small series of tribes derived from Tindale's study (1940) suggests that when small corrections are made for under-counting, that the Australian tribe may average about 10 bands. Assuming the tribal population to actually average 500 persons gives an average band population of 50. This value is exceeded in some favorable areas, but it certainly is considerably higher than the real figure in other lower density regions. It can be used for this preliminary study without too much distortion.

In both figures 1 and 2 it has been assumed that tribal boundaries will inhibit neither the interband exchange of women or the frequency of interband social relations and cultural contacts which are presumed to follow the same pattern. For-

tunately the data exist for correcting this assumption. Tindale, to whom anthropologists owe so much for detailed and quantitative knowledge of Australian aboriginal anthropology, published (1953) an exhaustive study of the rates of intertribal marriages among individuals prior to the distorting influence of white contact. These data were based upon geneological materials and have been analyzed with meticulous care. While there are some slight regional variations in rate, the continental average was 14 per cent intertribal marriages of the total number recorded. This figure not only provides the human microevolutionist with an invaluable basis for estimating the rate of gene flow via migration but here gives an opportunity to estimate the intensity of the barriers against cultural exchanges which in fact do exist at tribal boundaries. The existence of such barriers may be postulated in an a priori sense from the very existence of the clusters of homogeneous bands known as tribes. Without an inhibiting influence at the tribal boundaries these aggregations of local groups could not maintain their homogeneity but would in fact dissolve into an unstructured band space.

A mean figure of 14 per cent extra-tribal marriage among precontact Australians allows an estimate to be made of the cohesive factors which produced tribal entity. In terms of the idealized geometry of hordes of hexagonal configuration, a tribe with 10 hordes would be expected to show about 52 per cent extra-tribal marriages if the tribal boundaries exerted no cultural inhibiting forces. The fact that only 14 per cent do occur indicates that 3.7 times as many marriages might be expected without the interference of these factors for internal cohesion. In areas where tribes average 15 bands apiece, about 44 per cent of extra-tribal marriages would be expected, which gives the value of 3.1 for this index. For tribes which, on the average, comprise of about 5 local groups the index rises to 4.6, owing to the nature of the geometrically based relationships of the band. This index, which measures the expected number of extra-tribal marriages, should factors of cultural cohesion not disturb them, as compared to those which actually occur, might well be called the marital index of cultural cohesion. Even though the average number of bands per Australian tribe is but scantly documented, it certainly is contained within the range between 5 and 15, and this corresponds to index values ranging roughly from 3 to 4½ times for the cohesive influence. It is to be noted that this index applies only to Steward's unilineal band structure, in which the local groups are both patrilineal and exogamous. Even so, it is applicable to a large proportion of the peoples at this economic level of subsistence.

Model for Social Rates of Band Interactions

In the previous model, based upon the geometrical distribution of bands in space, the direction of the forces involved is evident. This geometry works so that an increase in the number of bands in a tribe further insulates it from extra-tribal cultural influences and so would tend, working by itself, to increase the number of bands per tribe. In the reverse sense, tribes containing too few bands, unless isolated by topographical or ecological features, tend to be exposed to an undue number of extra-tribal influences culturally, and so would find it difficult to maintain a homogeneous core of cultural values. It may be postulated that below this threshold tribes would tend to disappear through absorption by neighboring and more stable groups.

The force opposing this tendency to increase the number of bands per tribe is based in another aspect of the geometry which involves distance. The influence of distance can perhaps be best examined through models which synthesize the total social and cultural interactions of a band in the central position in a tribe in terms of contiguous and non-contiguous bands

within the same tribe, and those extra-tribal bands which it may occasionally interact. Again, it is unfortunate that field observers provided very little empirical data as to the nature and frequency of such contacts. For Australia, and these conditions presumably hold reasonably elsewhere, a given band may be expected to have most frequent contacts with those local groups which share its boundaries. Less frequently it will meet with local groups of its own tribe but one band removed from its territory, and upon rare occasions it may be expected that it will come into face-to-face contact with bands from outside of its own tribal group. Contacts between adjacent local groups no doubt frequently occur without the excuse of formal ceremonial occasions. But contacts with more remote bands are primarily a consequence of invitations to participate in ceremonies of various sorts. This is not to say that other occasions, such as trading parties and revenge parties do not play a role in these contacts between bands, but it may be safely presumed that they are less frequent and less important for the purposes of our model. Correspondingly they are ignored in these tentative versions.

The variables used in the construction of the following models fall under five headings: (1) geometry of bands in space; (2) frequency of interaction; (3) intensity of interaction; (4) duration of interaction; and (5) facility of communication. Each of these factors will be discussed separately below.

The influence of the geometrical spatial relations of bands has been explored previously in figures 1 and 2. For this model the hexagonal configuration will be utilized since this seems to correspond more closely to actual conditions. In such an arrangement of bands the one centrally located within the tribe, which is here being considered, will have direct territorial contacts with the 6 contiguous bands about it. These contacts will be frequent as the local groups go through the seasonal rounds within their own territories. Spaced about these contiguous bands are 12 local groups once removed from the central one, and here the contacts will be more formal and less frequent. Thus in this configuration a tribe is considered to consist of 19 bands in all, a figure which is somewhat larger than that attained on the average among Australian tribes. Finally, outside of the tribal territory but contiguous to its boundary, are 18 bands which in this model belong to the 6 adjoining tribes. The central band will have infrequent contacts with these extra-tribal local groups, and only upon such occasions has involved the performance of inter-tribal ceremonies. Thus, for model purposes it is considered that the central band of the tribe may come into contact with 36 other bands, with varying rates of frequency.

The frequency of interaction between the central band and those once, twice and thrice removed from it certainly occur as an inverse function. Three sets of assumptions have been utilized in figure 3, based upon the following estimates of frequency. In the first instance it is assumed that the central band will have individual contacts with each of the contiguous bands once each year, that it will have social contacts with the bands once removed on the average of every second year, and it will contact extra-tribal bands only every fourth year. Empirical data on actual frequencies, as mentioned previously, are extremely scarce in the literature, but they make it quite clear that this is the most likely of the three assumptions to approximate the true situation. The second assumption involves more frequent contacts with more distant groups in the following way: contacts with contiguous bands remain one per year for each band; contacts with tribal bands once removed are increased to one each year; and extra-tribal band contacts are presumed to occur every second year. This assumption seems less likely since it tends to over-emphasize the frequency of social contacts with bands geographically re-

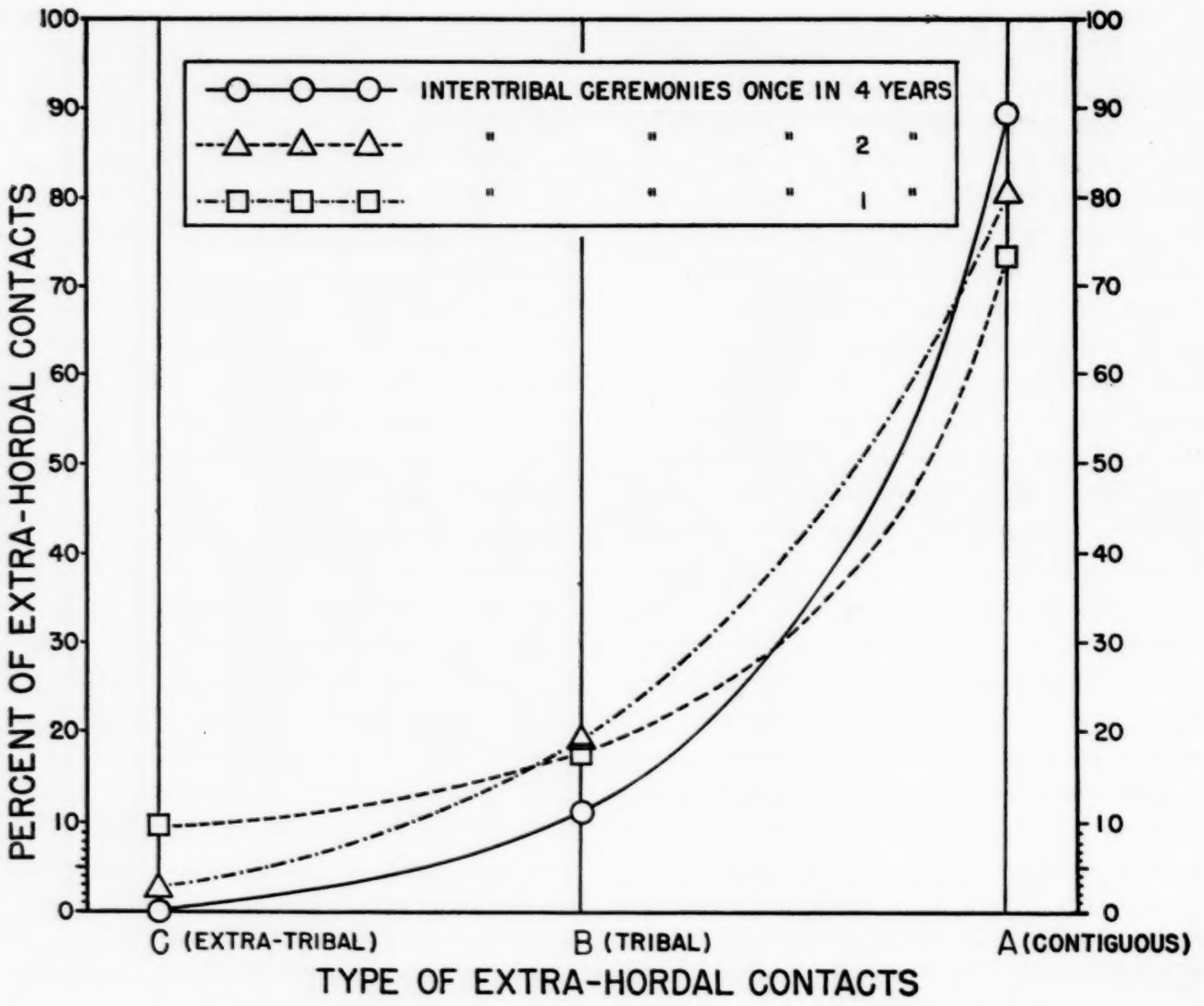

FIG. 3. Diagram of relationship of type and per cent of extra-hordal contacts. For explanation see text, pp. 201–204.

mote. The third and least likely assumption considers that contacts will be established once each year with bands in all three of the previous categories. This is not a realistic estimate and it is included only to provide an extreme limit for the phenomenon investigated.

In these preliminary models the intensity of interaction is defined simply as an inverse function of the number of other bands present. For the purposes of this construct, it is assumed that contiguous bands are in effect all seen together, and that the rate of intensity of interaction for any given band is $\frac{1}{6}$. Where the whole tribe gathers, an event probably rare in actuality, there are 18 bands present, and it assumes that the central band interacts with the intensity of $\frac{1}{18}$ with each of these. For an intertribal ceremony in which the 36 bands are assumed to be present, the intensity of interaction would be $\frac{1}{36}$ with each of the bands. This is conservative in that field data do not suggest that in intertribal ceremonies one-half of the participants are extra-tribal in origin.

The duration of interaction, while a theoretical component of the model, must be ignored in its actual construction. Important ceremonial events occasionally are recorded as continuing through 3 or 4 months, but there is no evidence to indicate how frequently such ceremonies were held. In a general way it is clear that at a generalized hunting and collecting level of economy such an event must be very rare for the food resources available to support such a large gathering for such a protracted period of time would limit the

number of possible occasions. This factor is omitted, but with the understanding that it would tend to be inversely related to the factor of frequency and so to level out the influence of that variable.

Facility of communication is a measure of linguistic similarity or difference. There seem to be no data to indicate proper values for this factor, but since tribes owe their existence to linguistic and cultural homogeneity, the differences between the bands of the tribe cannot be great. For the purposes of the present model, using unity as a measure of the linguistic facility of communication within a band, it is considered that this facility might diminish to .9 for communication with adjacent bands. For bands once removed the fact has been reduced to .7 and for extra-tribal bands, those twice removed, the factor is reduced to .5. The last factor is based upon the common native description of the language of adjacent tribes that "I can hear him but I can't talk to him." It is probable that the first two values should be somewhat higher, but since this factor has relatively little influence upon the curve derived from the total series of factors, the values can stand at these levels.

If it is assumed that the total social interactions of one horde with all other hordes with whom it makes occasional contacts remains essentially constant when assayed over long periods of years, then it is possible to establish a measure of the relative frequency of contacts of the three different kinds discussed above. The equation in its simplest form is:

$$K = (f_a)A + (f_b)B + (f_c)C$$

The constant A designates the proportion of interactions with immediately contiguous bands, the constant B shows interactions with other bands in the tribe but once removed from the central band, and C represents the relative rate of social interaction with local groups outside of the tribe. The variables f are composite and each includes the five factors discussed earlier in this section. Thus (f_a) includes g_a, f_a, i_a, d_a, c_a, which represent respectively the geometry, frequency of interaction, intensity of interaction, duration of interaction, and facility of communication. Thus the equation fully expanded stands as follows:

$$K = g_a f_a i_a d_a c_a A + g_b f_b i_b d_b c_b B + g_c f_c i_c d_c c_c C$$

The substitution of empirical values in the equation requires a further explanation. Contacts with contiguous bands occur locally, at tribal gatherings and at the great intertribal ceremonies. Interactions with local groups once removed occur only in the latter two occasions. Extra-tribal band contacts require intertribal ceremonies to come into being. Using the first assumption, which concludes with extra-tribal interactions occurring only once in four years, the equation becomes:

$$K = 89.05 \text{ per cent } A + 10.66 \text{ per cent } B + 0.29 \text{ per cent } C$$

Using the second assumption in which frequency of extra-tribal interaction is increased to every second year the equation stands as:

$$K = 80.23 \text{ per cent } A + 19.20 \text{ per cent } B + 0.57 \text{ per cent } C$$

Using the third and most extreme assumption in which intertribal ceremonies are presumed held every year with regard to the bands in question the equation reaches the values of:

$$K = 73.13 \text{ per cent } A + 17.50 \text{ per cent } B + 9.37 \text{ per cent } C$$

These three calculations have been graphed in figure 3. Since type A and B interactions combined represent intratribal contacts and only type C represents extra-tribal social interaction on a relative scale of 100 per cent, it is highly significant that under the most likely set of assumptions, that is the first type, these extra-tribal contacts amount to 0.3 per cent.

Even under the second set of conditions they only rise to 0.6 per cent. The totally unrealistic assumptions of the third type yield a value of less than 10 per cent extra-tribal interactions. Even without the detailed empirical data of the kind that would allow the equation to be calculated accurately, it becomes evident that without introducing inhibiting factors of tribal boundaries to reduce the interaction rates with extra-tribal bands, that distance itself reduces the rate to almost unimportant values. A proper correction for the actual inhibiting factors that do exist at tribal boundaries would even further reduce the relative rates of social and cultural intercourse with extra-tribal groups.

Thus the model for rates of band interaction, which are based upon a geometrical function of distance, demonstrates the nature if not the actual values of the force which acts in primary opposition to that previously discussed under the model on geometry of band relationships. It would be an oversimplification to claim that the tendency for tribes among generalized hunting and collecting peoples to approach a stable population number is the result of these two forces alone. Certainly other kinds of factors operate to keep the equilibrium stable. But it is perhaps not claiming too much to say that the two discussed here are perhaps of primary importance in the network of forces which maintain the general equilibrium values.[2] If refined empirical data were available, it might prove possible to express the two forces in terms of numbers of bands and equate them for the equilibrium conditions, and so calculate the numbers of bands expected under the simplified two force system for internal cohesion.

[2] The regions of tribal fragmentation in Australia which seem primarily associated with the recent acceptance of the iniatory rites of circumcision and subincision, and secondarily with low reliability of rainfall (Birdsell, 1953), may ultimately be explained in terms of these two vectors. If these rites are diffused (by formal and positive introduction) to portions of tribes, then the phenomenon of transient fragmentation can be interpreted as a consequence of a disturbing force which is corrected with the passage of time, by the ever present major forces producing stability in the size of the tribal population. The general pattern of the spatial distribution of fragmentation corresponds to an age-area theory based upon the above considerations.

Conclusions

Despite the appalling lack of detailed quantitative data upon which generalizations can safely be based, it is to be concluded that generalized hunting and collecting populations, as defined in this paper, show further regularities than those previously observed in anthropological literature. Under the general theme of territoriality two detailed studies, one in Australia and the other among the Great Basin Shoshoni indicate that human densities at this economic level are primarily determined by environmental variables which act in rigorous fashion. Ecological considerations for other such populations suggest that though the variables may become more complex, they operate just as stringently. The corollary of this finding is that populations of hunting and collecting peoples are essentially stable (but not to the extent of barring minor oscillations) and are in equilibrium with the carrying capacity of the country, as determined by the extractive efficiency of the population in obtaining energy.

Under the subject of population dynamics it would appear that such economically simple populations may be expected to show an intrinsic rate of increase which involves doubling their numbers in each generation, when placed in an unlimited environment. Consideration of the prolonged period of nursing and generally high infant mortality lead to the conclusions that the effective number of offspring of such populations shows a low and essentially constant variance so that the equation which relates effective size of the population to the size of the breeding population is simplified into a direct relationship between these two values.

A preliminary exploration of some of the factors making for social cohesion indicates that the stability observed in the size of tribal populations among such peoples may be primarily related to two opposing forces which have their basis in spatial geometry. A simple model based upon a hexagonal configuration for band geometry shows that tribal cohesiveness is increased as the number of bands increase. At the same time it is possible to measure for Australia the cultural inhibiting forces exerted by tribal boundaries in terms of extra-tribal marriages. On the assumption that Australian tribes approximate 10 bands on the average, it was found that 3.7 times as many extra-tribal marriages should occur according to geometry as do occur, if no barriers to them existed at the tribal boundaries. In another type of model, which represents a crude assay of the character of rates of interaction between bands it is possible to show that under any set of reasonable assumptions a centrally located band in a tribe has a negligible portion of its total interaction with extra-tribal local groups. This model demonstrates the great importance of distance in opposing the enlargement of the number of bands within a tribe. It is hoped that with more empirical data it will be possible in the future to develop series of quantitative studies which not only more accurately define the stabilizing factors discussed in this paper, but perhaps to explore other less important ones which certainly exist.

Acknowledgment

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PROBLEMS OF CULTURAL EVOLUTION [1]

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This paper is concerned with the biological factor in cultural evolution, with possible ways in which inherent physical, physiological and psychological characteristics shared by all human beings have conditioned culture and channeled the direction of its development.

About thirty years ago, Clarence Day wrote a whimsical and provocative little book entitled "This Simian World." He speculated about what human beings would be like if they had evolved from orders other than the primates. Descended from felines, he suggested, they would be fiercely jealous, and from bovines they would be placid and unimaginative. But, derived from the primates, they are insatiably curious and given to scrutinizing, manipulating and inventing things.

This charming speculation suggests that the inherent characteristics of mankind have perhaps been so obvious as to be overlooked. Not that there is anything new in enquiries about "human nature." But when human nature is examined in the light of its extremely diversified manifestations in the many different world cultures, there is a strong tendency to emphasize the cultural variable and to ignore the biological constant. This is true even of the recent culture and personality studies, which are interested in how what are presumably the same psychological processes manifest themselve in different cultural personalities.

In approaching this problem, it is important to distinguish the organic human factors which make culture in a general sense possible from those which may help explain particular and differing patterns of cultural behavior.

The organic preconditions of culture—the developed brain, speech center, hands, bipedalism, and other human characteristics—have been set forth in a separate paper in this symposium by Washburn and Avis. These enabled man to develop language, but they do not explain particular languages. They permit inventions, but since each invention is a rational solution to particular problems, they cannot tell us what things men will devise. For these reasons, there has been a tendency for some scholars to argue that the specific inventions or innovations, languages, and behavior patterns which distinguish the various cultural traditions or culture areas of the world must be explained solely by cultural events, by culture history, and on a purely culturological level without reference to the inherent or organic factor.

The remarks that follow are intended to point up the importance of the human common denominator rather than to suggest substantive conclusions. It is certain that there are limits upon the range of cultural behavior, although these have never been specified. It is also true that the distinguishing chararteristics of particular cultures are really a combination of cultural-historic factors and biological factors. The contention that the latter are extremely important is consistent with a recognition that they always operate in conection with traditional or socially inherited patterns.

Some of the cultural implications of man's inherent make-up have previously been suggested, although they have not been followed up. Twenty-five years ago,

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Zukerman (1932) called attention to the importance of the primate sexual cycle to human society. That primates, unlike other animals, have a fairly constant sexual urge rather than seasonal rutting is one of the critical factors in the universality of the nuclear or biological human family. The need to care for children through their many years of comparative helplessness, which is another biological factor, also gives the family a vital function. While this care might be accomplished through other social arrangements, modern attempts to socialize child care seem always to have failed. The nature of human sexual activity is clearly a very real factor in delimiting the range of cultural forms that the nuclear family takes, even though extended family relations vary considerably. The prolonged human infancy also is a factor in sexual division of labor which assigns women household chores and other tasks that do not take her far from home.

Washburn and Avis' point that *Homo sapiens*, unlike the other primates, is carniverous, invites speculation beyond the interesting suggestions of these authors as to its effect upon culture. While carniverous habits, like other biological factors or potentials, operate only in the context of particular cultural and environmental circumstances, its effect is very positive and real.

The importance of carniverous habits in bringing social cooperation is strikingly evidenced by the contrast between the fairly tight-knit hunting bands of the native people of Canada, Australia, South Africa, South America and elsewhere with the independent family units found among food collectors such as the seed-gathering Shoshoni Indians of Nevada and the shellfish gatherers of the Chilean archipelago (Steward, 1955). In both hunting and collecting societies, the nuclear family exists because of the organic factors of sexual behavior and prolonged infancy, combined with the sexual division of labor. The hunting bands are conditioned by the further organic fact that man will eat meat if he can get it and that cooperation increases the take in hunting whereas seed gathering in areas of limited resources puts individuals in competition with one another.

The carniverous habit alone does not explain the nature of hunting bands. Man must also have technological devices, such as bows, spears, traps, nets, and others; and the manner in which he organizes in order to employ these devices depends upon the game itself. A prolonged collective drive to hunt large migratory herds of caribou entails different organization than that needed for a brief rabbit drive.

In some cultures, manifestations of what may be basically carniverous habits extend much farther. The Chibchans of Colombia, the Carib of the Antilles, the Tupinamba of Brazil and many other primitive people had a most sanguinary pattern of warfare wherein captives were tortured, slain, and eaten. In some cases, their heads, whole skins, or bones were made into trophies. In this pattern, as in the others mentioned, the question is not whether the organic factor automatically and invariably produces cultural patterns. Obviously it does not; for many societies are eminently peaceful; and some, like the modern western nations, place great value on human life—except in times of warfare.

The varieties of warfare require attention to the cultural historical factors. In modern times, warfare is motivated by the desire to conquer people or to control their wealth. Perhaps this economic competition also rests upon a biological basis, although one need not follow the older psychologists in postulating an instinct of avarice.

In some of the bloodthirsty primitive patterns of warfare which have no economic motivation, another inherent human characteristic must be considered. Among the members of close-knit families and small societies, any hostilities must normally be suppressed lest the in-group be disrupted. Culture may provide dif-

ferent means of release for these pent-up aggressions in non-disruptive ways.

One cultural outlet is the kind of warfare just mentioned. This pattern is best exemplified by the Tupinamba Indians of South America (Métraux, 1948), who raided their neighbors in order to take captives whom they first adopted as members of the captor's family, then tortured, killed and ate. It is interesting that the Tupinamba so stressed harmonious relationships within the community that anger was a cause for great shame while a quarrel might lead the transgressor to burn down his own house or commit suicide by eating earth.

The practice of making a war captive the surrogate or scape goat for in-group hostilities is not unique among the Tupinamba, although few people carried it out with such frenzy. The Iroquois and their neighbors also forced war captives into a similar role.

This analysis undoubtedly oversimplifies the problem. On the one hand, there are other culturally-derived factors, such as religious beliefs or a drive for prestige, which motivate warfare. And many people do not torture or kill their captives. On the other hand, while culture may provide for the release of hostilities by such means as hurling verbal insults in formal exchanges and duels as well as captive-taking and human sacrifice, it may handle them in other ways.

The age-old belief in witchcraft is one cultural device for suppressing open aggression under certain circumstances. In recent years, influences from the larger economic world have tended to change Navajo land use from one of common ownership to individual ownership and to increase the individually-owned herds of sheep. But the strong belief that anyone who increases his fortunes at the expense of his fellows will be a victim of witchcraft has been a strong deterrent to the new trends. Open competition for wealth has been inhibited by this fear. In Puerto Rico (Padilla, 1956), the north coastal plains are overpopulated by sugar workers who cannot find sufficient employment on the government-owned, profit-sharing plantations. The overflow of excess mountain population into this area meanwhile intensifies the underemployment and places the people in bitter competition for jobs. The antagonism engendered by this competition is expressed as fear of witchcraft rather than in open conflict. Such fear has been a factor in eliminating open competition in many societies throughout history.

Another culturally-derived means of deflecting aggression is certain patterns of drunkenness. Among the Northern Paiute, brothers-in-law are normally the closest friends—closer, in fact, than brothers. One day, however, two brothers-in-law began to drink and within an hour attacked each other with every intention of murder. The basic hostilities were clear, but there was no patterned means for releasing them. The Inca Empire, on the other hand, apparently with considerable awareness of the deeper implications of drunkenness, encouraged the common people to alcoholic excesses during the great religious festivals. On these occasions, the accumulated resentment of the people toward the state as well as toward one another, could be diverted into religious frenzy. A very different but equally effective religious outlet is found in modern revivalistic cults, where group participation provides an emotional safety-valve for persons frustrated in their earthly ambitions.

There are probably many other cultural mechanisms or patterns that meet this inherent human need to drain off aggressions. The need for substitutes for physical violence against the competitor may involve villages or states as well as individuals. In aboriginal Meso-America, local groups competed in a fairly complicated ball game played in large, walled courts. This, like many modern athletic contests, has been described as "the moral equivalent of warfare." In this connection it is worth noting that games everywhere are essentially competitive, as are

many play patterns of children, and that these are more like those of young carnivores than herbivores.

A very different subject matter that also illustrates the role of the inherent human or organic factor as a condition and partial explanation of culture is found in humor. Nearly thirty years ago, in an unpublished doctoral dissertation, I analyzed the themes of humor that cut across the different cultures of native North America (Steward, 1931). While clowning was carried on in such different contexts as the organized societies of the Pueblo Indians or the informal groups among the Plains Indians whose members became clowns because they were thought to have been struck by ligthning, certain basic subjects were universally a cause of laughter. In all cases, the clowns indulged in sexual pranks that were normally forbidden. In all, they impersonated quarreling and bickering spouses and played scenes of domestic strife that would have disrupted any family. They limped about as sick, lame and starving beggers. They defiled sacred objects, broke religious taboos, and interrupted ceremonies. And they burlesqued and ridiculed persons of foreign groups and cultures.

While there are many theories of humor, ranging from Crile's psychological theory through Bergson's philosophical approach to dozens of psychological theories, including that of Freud, all postulate some inherent characteristic of human beings. These themes of humor are familiar in Western European culture, and they all involve circumstances that would be socially and psychologically disastrous if real but are correspondingly funny when done in jest. My own study dealt with the institutionalized clown, which was somewhat patterned in each culture by different religious functions and rather formalized behavior. Nevertheless, the comic performances were strikingly similar, and spontaneous, every day humor appears to be based on much the same themes.

By way of conclusion I would like to emphasize again that the significance of the organic factor in cultural evolution depends upon how one conceptualizes culture. Someone has said that any characteristic shared by all cultures is organically determined rather than culturally determined. Language is an expression of an organic potential while a particular speech results from culture history, and dancing is an expression of inherent capacity for body movements and rhythm while particular dance forms are culturally derived. By this definition, culture is that which distinguishes the behavior of human societies.

This distinction does not, however, imply that the varieties of culture can be explained solely on a cultural or superorganic level. That a person like A. L. Kroeber is interested in cultural phenomena and their history, and believes that anthropology should deal only with the superorganic, is not arguable. Nor, I submit, is there room for contention that it is equally justifiable to seek explanations on a deeper level and in whatever directions they may lead.

My point has importance in the perspective of evolutionary approaches to culture. The nineteenth century scholars sought general or universal explanations of culture change. As it happened, their explanation was the philosophical hypothesis that there is inherent tendency for progress. In reaction to the belief in the original creation, acceptance that culture had evolved from primitive "savagery" to "civilization" just as life had developed from very simple forms to the higher organisms was interpreted as inevitable improvement. But twentieth century attention to detailed cultural differences led to stress on the uniqueness of each tradition or culture area and negated generalizations.

In the last two decades, interest in evolution has revived, and, while it has taken several forms, I think it is still characterized by a search for causal explanations. If we define culture as that

which distinguishes societies, we must conclude that any universal explanations will be found in organic factors. Just how these factors have imposed limits on the range of cultural variation, how they have channeled directions of the evolution of any culture and how they have interacted with cultural forms to give the latter special function and meaning is our fundamental problem.

Surely this simian world, and more especially this human world, is not one in which culture evolves as if there were no people.

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RECENT CHANGES IN THE INTRODUCED POPULATION OF THE FIRE ANT *SOLENOPSIS SAEVISSIMA* (FR. SMITH)

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Introduction

A reconstruction of the history of the imported fire ant population in the southern United States, from the time of its introduction around 1918 until 1949, has been presented by one of us in earlier papers (Wilson, 1951, 1953). Briefly, it was shown that the population consisted for the first ten years or so of a "dark phase," corresponding to the southernmost geographic variant of the South American mother population. During this early period the species was unable to spread outside the limits of Mobile, Alabama, the port into which it had been introduced. Around 1930 a second form, lighter in color and smaller in size, made an appearance and in the ensuing twenty years rose to predominance in the population. With the appearance of the light phase, the species as a whole commenced a rapid spread, until by 1949 it occupied a broad area encompassing several counties in adjacent parts of Alabama, Mississippi, and Florida. The light phase is morphologically identical to a geographic variant from a central sector of the South American mother population. In the United States it has interbred completely with the dark phase to produce a graded series of intermediate forms, of such a nature as to suggest that the two extreme forms differ by polygenes.

In 1949, when *S. saevissima* began to receive a great deal of public attention as an insect pest, a survey program was started by the Bureau of Entomology and Plant Quarantine of the United States Department of Agriculture, and this agency has been following closely the spread of the introduced population since then. In 1956 and 1957 the present authors returned to the infested area to carry on further ecological work and to determine whether significant shifts in the frequencies of the color phases have occurred since the time of Wilson's original study in 1949. Additional, more limited studies were made at this time on the effects of competitive pressure from *S. saevissima* on the native species of *Solenopsis*. The results of this recent work form the material of the present paper.

The Continuing Spread of the Population

Figures 1 and 2 show the spread of *S. saevissima* since its introduction around 1918. It will be noted that the ant has been increasing its range by two means: steady expansion of the main population outward from its center at Mobile, and establishment of isolated, secondary populations beyond the limits of the main population. The main population has been growing outward rather constantly at a rate of approximately five miles a year, undoubtedly through the primary agency of nuptial flights and subsequent founding of colonies by single fecundated queens. The secondary populations are usually founded by lone queens or fragments of colonies carried in nursery stock, as shown by the work of Culpepper (1953). With time, some secondary populations have expanded to the point of fusing with each other or with the encroaching main population.

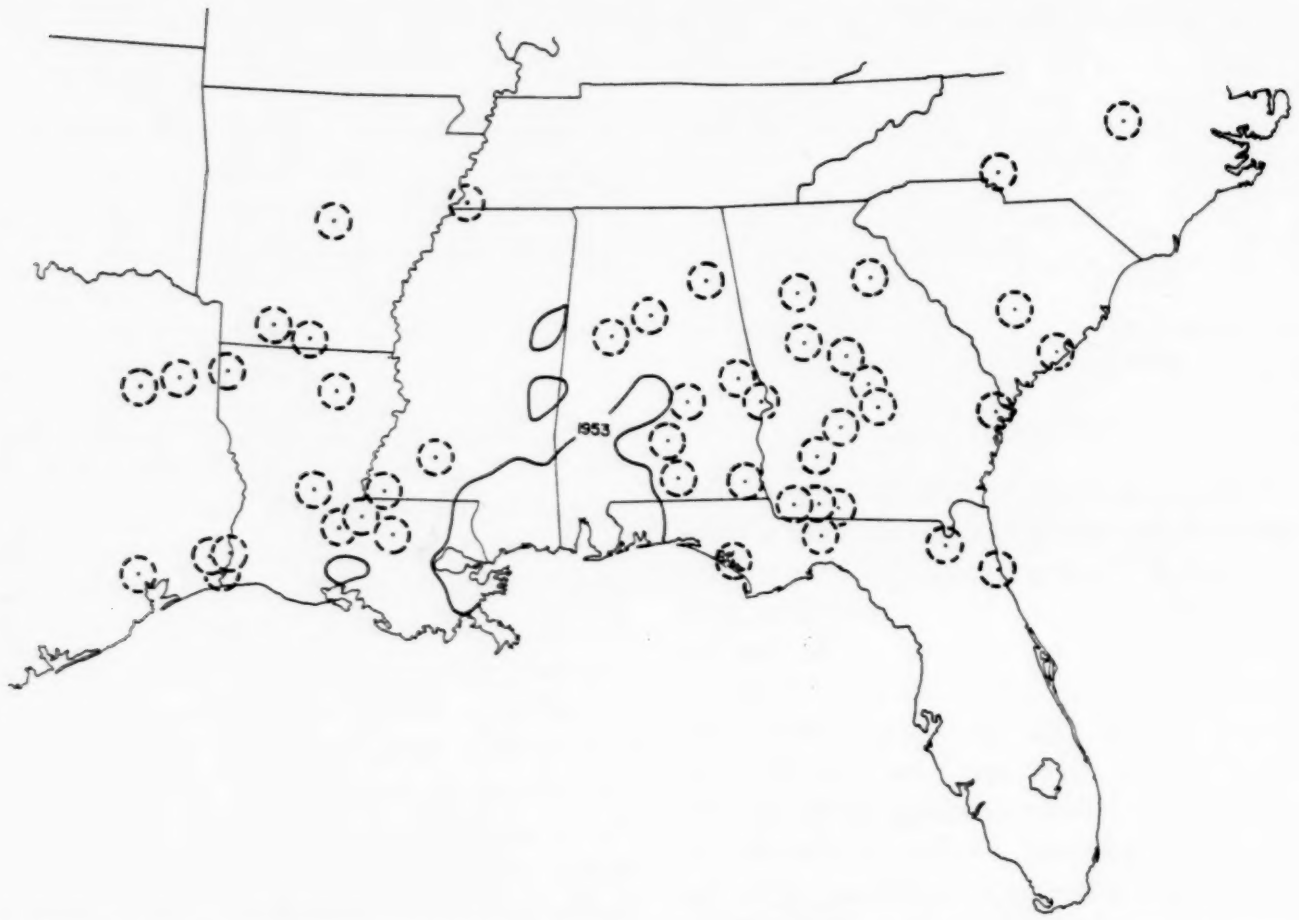

FIG. 1. Distribution of *Solenopsis saevissima* in the United States in 1953. The broken circles represent small secondary populations, mostly centered at and limited to commercial nurseries. The main area of infestation and three secondary populations in Mississippi and Louisiana are more extensive, and their limits more precisely known, so that they are indicated by solid lines. (Adapted from Culpepper, 1953.)

THE GENETIC BASIS OF THE VARIATION

The extreme color forms differ from each other in other characters, notably development of the gastric spot, total size, size and form of the nest, and certain details of habitat selection (Wilson, 1951). It was suggested originally that the difference is based on polygenes acting pleiotropically. This hypothesis must now be revised in part. A study of the South American population of *saevissima* has revealed that the three principal morphological characters show discordant geographic variation (see Wilson, 1952, for a partial description). Specifically, ground color darkens along a north-south cline, total size is smallest near the center of the population and increases both northward and southward, and the size of the gastric spot tends to show an irregular pattern of local variation. A closer examination of the intergrading extreme color forms at Gulf Shores, Alabama, in 1956–57, showed that ground color and gastric spot variation are only partly correlated. These data suggest that while variation of morphological characters may be under polygenic control, the polygene systems of the individual characters are partially or wholly independent of each other. There is not yet enough evidence to determine whether the same consideration applies to the ecological and ethological characters.

THE CONTINUING DECLINE OF THE DARK PHASE

In 1956–57 visits were made to several localities where the frequency of color phases had been determined in 1949, in order to learn whether the frequency had shifted in the intervening period. In

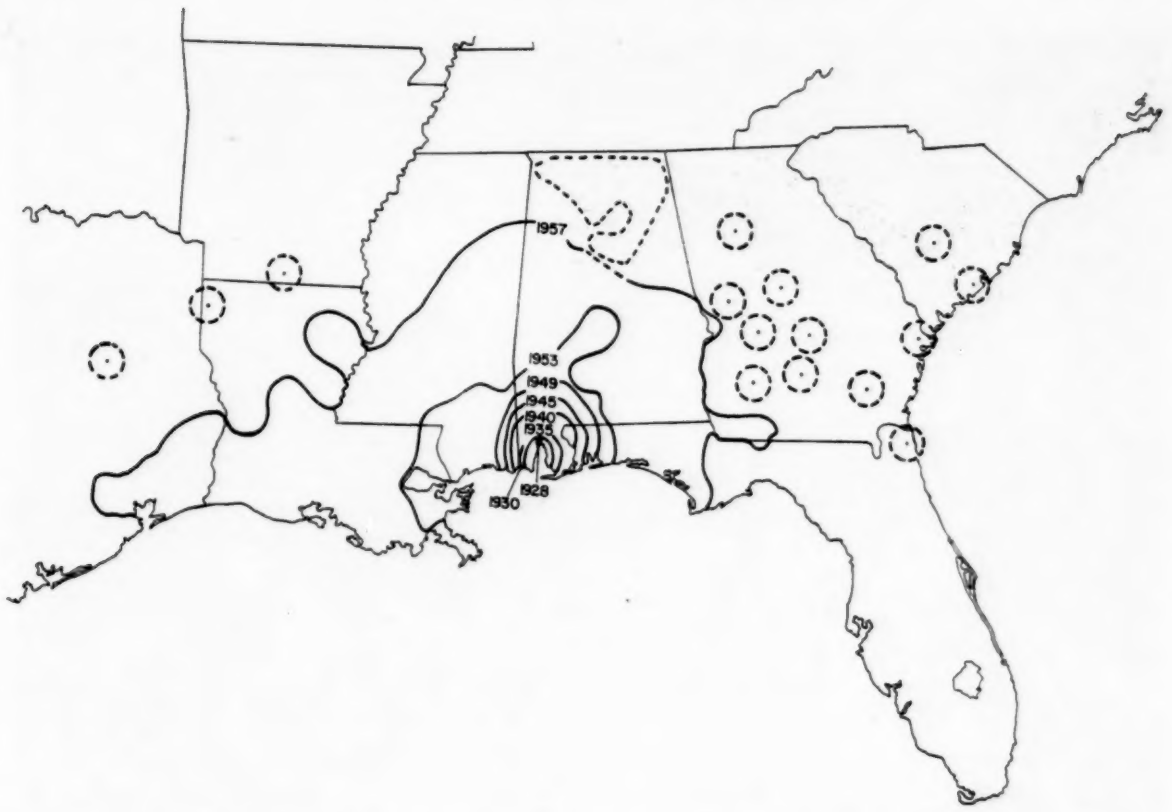

FIG. 2. Spread of the main area of infestation of *Solenopsis saevissima,* indicated by solid lines. Broken lines delimit secondary populations, mostly restricted to the vicinity of nurseries, as known in 1957. The distribution of the main population in 1957 as indicated here is not strictly comparable to that shown for earlier years, since the internal structure of the population now occurring over this much wider area is known in less detail, so that the extreme limits may enclose some secondary populations that were still isolated in 1957. (Adapted from Wilson, 1951; Culpepper, 1953; and recent records of the U. S. Department of Agriculture.)

TABLE 1. *Comparison of frequencies of dark and light phases in 1949 and 1956–57 in selected localities within the range of the introduced population*

Locality	1949		1956–57	
	Dark	Light	Dark	Light
Beach Road, Gulf State Park, Alabama	0.80 (8)	0.20 (2)	0.39 (7)	0.61 (11)
Main Road, Gulf State Park, Alabama	0.67 (2)	0.33 (1)	0	1.0 (13)
Foley, Alabama	0.70 (7)	0.30 (3)	0	1.0 (11)
Ft. Morgan Road, 1.6 mi. west of Gulf State Park, Alabama	0.40 (2)	0.60 (3)	0	1.0 (3)
Ft. Morgan Road, 7.7 mi. west of Gulf State Park, Alabama	0	0	0	1.0 (2)
Ft. Morgan, Alabama	0	0	0	1.0 (1)
Lowndes and Noxubee Counties, Mississippi	1.0 (20)	0	1.0 (15)	0

* Enclosed figures are absolute numbers of colonies. It should be noted that with the exception of the data for Lowndes and Noxubee Counties the figures given pertain to all or nearly all of the colonies at a given locality, and not to a random sample drawn from a larger population.

FIG. 3. Dark-phase fire ants in the Artesia, Mississippi, population. *Upper:* mound nest in the vicinity of State College, Mississippi, showing the relatively abundant thatching characteristic of dark-phase nests. *Lower:* dark-phase workers removing sexual prepupae from an exposed nest gallery. Note the deep body ground color and (on upper left worker) the extensive light patch on the first gastric segment. (Photographs through the courtesy of Dr. Ross E. Hutchins, Mississippi State College.)

almost every locality a significant decline of the dark phase was noted, in two instances amounting to complete extinction and replacement by the light phase. Before describing these findings, it should be observed that the older color classification of Wilson (1951) has been modified in the following two ways. (1) In view of the genetic independence of the morphological characters, the classification is now based on ground color alone, rather than ground color and gastric spot size in combination. (2) The subjective, arbitrary divisions have been reduced from six to two. "Dark phase" as used here includes the "extreme dark" and intermediate phases of the 1951 classification, while "light phase" includes the former "dark red" and "light red" categories. Both of these changes involve simplifications, but no changes in essential criteria, so that the 1951 and present classifications are parallel. Below are described the color-phase compositions of several local populations in 1949 and 1956–57. Frequency data, when available, have been summarized in the accompanying table.

Gulf State Park, Alabama; beach road extending east from Park Casino. In March, 1949, the first ten nests on the roadstrips near the beach going east from the Park Casino, covering a distance of approximately one mile, were classified according to color. Eight were dark phase and two light phase. By 1956, the balance had shifted. In March of that year the first 18 nests encountered going east from the Casino, and covering almost exactly the same distance were composed as follows: 7 dark phase, 11 light phase. In June, 1957, at a time of year when the nests were difficult to find and the survey consequently less complete, only 10 nests were found along the one-mile stretch. These were composed as follows: 5 dark phase, 5 light phase. All of these data suggest that at this locality the dark phase colonies have changed little if any in absolute numbers during the past eight years, while those of the light phase have been increasing.

Gulf State Park, Alabama; main road. In March, 1949, the grassy strips bordering the portion of the main road leading through the wooded zone, from the main Park entrance to the border of the coastal marshes, were populated by an undetermined number of *saevissima* colonies, of which the dark phase formed a high percentage. In March, 1956, 30 nests, forming probably a large majority of all the nests along this portion of the road, were classified according to phase. Only a single one was dark phase. In March, 1949, at a point just 0.5 mile in from the main Park entrance, of three nests examined two were dark phase and one was light phase. In June, 1957, this spot and the roadstrip area for a distance of 200 yards in both directions [1] were explored intensively for *saevissima* colonies. Of 13 found all were light phase. It is clear that within seven or eight years the dark phase, originally abundant in this roadside area, has been all but replaced by the light phase.

South of Foley, Alabama, on State Highway 9. In March, 1949, 10 nests were examined in the grassy roadstrips and an open field 0.7 mile south of the town limit. Seven were dark phase and 3 light phase. In June, 1957, the same immediate area was surveyed, and of 11 colonies found all were light phase.

Fort Morgan Road, 1.6 miles west of Gulf State Park entrance. In March, 1949, this was the westernmost locality on the Ft. Morgan Road where *saevissima* occurred. Of five nests found here at that time 2 were dark phase and 3 light phase. In June, 1957, three nests were found at the same spot; all were light phase.

Fort Morgan Road, 7.7 miles west of Gulf State Park entrance. In 1957 two nests were found at this point on the Ft. Morgan Road, well beyond the known limits of the 1949 population. Both were light phase.

Ft. Morgan. Between the above lo-

[1] The surrounding pine-oak-palmetto forest contained almost no *saevissima* colonies.

cality and Ft. Morgan itself, few situations favorable for fire ants exist, and *saevissima* is evidently very scarce to absent. Ft. Morgan, located on the tip of the Ft. Morgan Peninsula, is partly covered by grassy lawns that could support *saevissima* colonies. After careful search of these lawns, a single light phase colony was found.

On the basis of the present limited evidence relating to the spread of *saevissima* on the Ft. Morgan Peninsula, it thus appears that the dark phase has declined, or completely disappeared, at the western edge of the species' 1949 range, and that the light phase has effected the subsequent invasion of the few suitable habitats over the rest of the Peninsula.

Vicinity of Meridian, Mississippi. In 1949 the isolated population centered at Meridian was apparently composed entirely of dark phase colonies (Culpepper, in Wilson, 1951). By the time of the authors' visit in June, 1957, this population had been overflowed by the main *saevissima* population, centered at Mobile and composed principally of light phase colonies. The resulting mixed population at Meridian contained large numbers of both phases, as shown by the following frequency data. Southwestern city limits, near the site of the General Box Company on U. S. 80: 1 dark phase. One mile east of above point on U. S. 80: 3 dark phase. Junction of U. S. 45 and U. S. 80: 1 dark phase, 2 light phase. Near center of city, 2 blocks northeast of the Hotel Lamar: 1 dark phase, 4 light phase. Three-fourths of a mile north of Meridian business district on U. S. 45: 6 dark phase, 6 light phase. Marion, 5 miles north of Meridian on U. S. 45: 5 dark phase, 2 light phase.

Lowndes and Noxubee Counties, Mississippi. The isolated population centered at Artesia, Lowndes Co., was definitely determined to be uniformly dark phase in 1949. In June, 1957, this population was still isolated[2] and apparently still uniformly dark phase. At Brookville, Noxubee Co., 8 nests examined were all dark phase (and with prominent gastric spots). According to one resident, *saevissima* first rose to abundance in the immediate vicinity of Brookville in 1955. Another resident stated that on his farm one mile south of the town *saevissima* had first been noticed in 1954 and was abundant by 1956. A third resident stated that the ant had made its appearance in farm country 4–5 miles west of Brookville in either 1953 or 1954 and became abundant there by 1957. All agreed that the nests were everywhere dark phase. This evidence suggests that the Brookville area has been populated by the southward-expanding Artesia population. Nests are abundant from Brookville north along U. S. 45. At Allandale, Lowndes Co., well within the range of the Artesia population, 7 colonies examined were all dark phase.

The Nature of the Selection

In 1956–57, particular attention was paid to the Gulf State Park population, where the dark phase has been in evident decline, in an attempt to determine which mode of selection has been in operation. One possibly significant biological difference between the phases was noted: incipient colonies (1–2 years old) of the dark phase are relatively very scarce or absent throughout the Park, even in the local areas where mature colonies of this phase have been relatively abundant since 1949 or earlier. It thus seems probable that most selection has been occurring at the early stages of the colony life cycle. This hypothesis is supported by the knowledge that ant species are generally most vulnerable at early stages of colony formation. Furthermore, it is well known that in at least some species a large percentage of nest- founding queens, and

[2] A very few colonies occur in intermediate localities on U. S. 45 between Meridian and Artesia. A single light phase colony was found just south of Lauderdale. Four other light phase colonies were found clustered together by the side of the road 2.3 miles south of Electric Mills.

probably young colonies also, are eliminated by aggression from larger colonies of the same species. That such a phenomenon also occurs in *S. saevissima* is suggested by the following facts: (1) Conflict and aggression are known to occur between mature fire ant colonies; (2) *S. saevissima* quickly and more or less completely replaces other fire ant species (subgenus *Solenopsis*) within its preferred habitats as it spreads, a situation that seems most likely to arise from intercolonial aggression.

Interaction with Other Solenopsis Species

The spread of the *S. saevissima* poputation has had a profound influence on the two native species of fire ants within its range, *S. geminata*[3] and *S. xyloni*. For *S. xyloni*, competition with *saevissima* has resulted in virtually complete extinction wherever *saevissima* has spread. *Saevissima* and *xyloni* can be found together only at the fringes of the *saevissima* populations, where *saevissima* has been present for only a year or so, as for instance at Perdue Hill, Alabama, in 1949, and Tuscaloosa, Alabama, in 1957. In eastern Mississippi, where there are still (in 1957) notable discontinuities in the *saevissima* population, *xyloni* apparently occurs only in enclaves where *saevissima* is scarce or absent. This mosaic pattern of distribution is evidently a result of the closely similar ecological preferences of the two species. Both are most abundant in open, grassy cultivated land, particularly roadstrips and pastures. Both are relatively very scarce in dense woodland.

S. geminata, on the other hand, shows broader habitat preferences than either *saevissima* or *xyloni*, and consequently has thus far fared better in competition with *saevissima*. In northern and central Florida, where the authors travelled in 1957, *geminata* is everywhere one of the most abundant and wide-ranging ants. Two color phases were found to occur over most all of this area, a light reddish form, often referred to in the literature as "subsp. *rufa*," and a blackish brown form, usually referred to as "typical" *geminata*. The relative abundance of each phase has not been determined, but our broad impression is that neither predominates heavily. Both occur together in some localities, as for instance Panama City. Intermediate forms exist, but these are less frequent than the extreme forms, and it has not been determined whether they form a complete graded series connecting the extreme forms, as is the case in *saevissima*.

The following ecological difference between the extreme color phases of *geminata* was noted. The dark phase occurs commonly in both woodland and open cultivated land; whether it favors either habitat cannot be determined on the basis of the data gathered in 1957. The light phase is primarily limited to open cultivated land, particularly grassy roadstrips, lawns, and pastures. Only a single colony was found in woodland, and this was in open turkey oak woods (*Quercus catesbaei*) near Galliver, Okaloosa Co., in the northwestern part of the state.

Both extreme forms occur abundantly through the Florida panhandle westward to the edge of the *saevissima* population. At Panama City, where in 1957 *saevissima* had been present for not more than several years, nests of both forms of *geminata* were found intermingled with those of *saevissima*. On the basis of direct comparison at this locality, the following possible significant behavior difference between *geminata* and *saevissima*

[3] *S. geminata* may possibly not be a native ant in the sense that it was present in the United States before the arrival of European settlers. Its present universal distribution in the West Indies, as well as over much of the Old World tropics, may indicate a rapid post-Columbian spread from its original range in Central and northern South America through the agency of human commerce. In any case, the distribution of *geminata* in the United States suggests that it arrived more recently than did *S. xyloni*, and that it may have replaced *xyloni* in wide areas in the Gulf States.

was noted: *saevissima* colonies are larger; the workers appear to be individually more aggressive, and they emerge from the nest faster and in much greater numbers when the nest is mechanically disturbed by a human observer.

Farther westward, within the area occupied by *saevissima* for more than several years, *geminata* is almost completely absent from the open cultivated land favored by *saevissima*. But it is still moderately abundant in denser woodland, where *saevissima* is scarce to absent. This ecological replacement pattern is reflected in a most interesting way on the genetic composition of the *geminata* population. The light phase of *geminata*, which elsewhere occupies the kind of habitat favored by *saevissima*, has been almost completely eliminated. *Geminata*, now primarily a forest-dwelling species, consists almost entirely of the dark phase. It thus appears that *saevissima*, while displacing *geminata* ecologically, has also displaced it genetically, to produce a marked new pattern of geographic variation. (For a general discussion of this kind of phenomenon, which we have called "character displacement," see Brown and Wilson, 1956.)

Summary

1. During 1949–1957 the main introduced population of *Solenopsis saevissima*, centered at Mobile, Alabama, continued to grow outward at an average rate of approximately 5 miles a year. Meanwhile, the total infested area in the southern United States was further vastly increased by the growth (and occasional fusion) of secondary populations beyond the limits of the main population.

2. The multiple morphological characters separating the extreme variants in the introduced population are probably under independent genetic control.

3. The dark color phase continued an overall decline during 1949–1957. The secondary population centered at Meridian, Mississippi, isolated and composed mostly or entirely of dark phase colonies in 1949, has since been overflowed by the northwestern portion of the main population, and in 1957 was composed of mixed light and dark phase colonies. The secondary population centered at Artesia, Mississippi, was still isolated and uniformly dark in 1957.

4. Selection between the light and dark phases appears to occur primarily at early stages of colony formation, very likely through the agency of intercolonial aggression.

5. The native fire ant *S. xyloni* has been almost completely eliminated within the range of *S. saevissima*. The native species *S. geminata*, which shows color variation parallel to that of *saevissima*, has survived primarily because its dark phase is able to nest in woodland, where *saevissima* is scarce to absent. Thus under competitive pressure from *saevissima* the sympatric population of *geminata* has been reduced both in its ecological range and in genetic variability.

Acknowledgments

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THE SIGNIFICANCE OF FLORAL CONSTANCY AMONG BEES OF THE GENUS DIADASIA (HYMENOPTERA, ANTHOPHORIDAE)

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The bee genus *Diadasia* Patton is a relatively large group of solitary or gregarious ground nesting species. It occurs only in the Western Hemisphere and is abundantly represented in southwestern United States and Mexico and in the arid and semi-arid portions of South America, but is rare in the moist tropics (Michener, 1954). Biological characteristics of *Diadasia* have been discussed elsewhere (Linsley, MacSwain and Smith, 1952, 1956; Linsley and MacSwain, 1957). It is the object of the present paper to emphasize the role that food habits and flower relationships may have had in evolution and speciation in the group.

As with most organisms, food habits have played an important role also in the evolution and speciation of bees. The choice of larval food, as is usually the case with plant feeding insects, is made by the adult. The bee larva, to survive, must accept the food since it is unable to make an alternative choice. The larval food is pollen, usually mixed with some nectar, gathered from flowers by the female bee. However, bees visit flowers for a variety of reasons, other than pollen collecting. Flowers provide adult food (especially nectar) for both sexes of all species, the site of mating for many, and a male sleeping place for others. Of all these functions, the collection of pollen by females invokes the most consistently specific response to flower species, although, in some cases, the mating search by males may be equally so. Bees in which the females are highly specific in their choice of pollen sources are termed oligolectic, those which are not specific, polylectic.

Flower constancy in the collection of pollen is a characteristic of bees in general. Two principal forms of constancy are involved. The first is characteristic of individual bees which, on one or several successive trips, may gather pure or nearly pure loads of pollen from a single kind of plant, although the species as a whole may be polylectic and not sharply limited in the kind and number of pollen sources utilized. This type of constancy has long been known to floral biologists, students of insect behavior, and research workers in certain production aspects of agriculture. It is characteristic of social bees (e.g. *Apis, Bombus, Melipona*), semi-social bees (e.g. *Halictus*), and many solitary bees (e.g., some *Anthophora, Andrena, Megachile*). The second kind of constancy was partially recognized by Loew (1886) and was more clearly defined by Robertson (1925).[1] It is adaptive in nature and is characteristic of species, genera, and even higher groups of bees. This form of flower constancy is

[1] Loew (1886) observed differences in the flower visiting habits of bees with tongues of about equal length (thus presumably with the same nectar sources available) and designated *monotropic, oligotropic* and *polytropic* types, depending upon whether they visited a single species of plant, related species of plants, or unrelated plants, respectively. Originally, Robertson adopted Loew's terminology but limited the application of the terms to flower visits for pollen. Later [Robertson (1925)] he proposed the parallel terms *monolectic, oligolectic* and *polylectic* for use in reference to pollen visits of bees, restoring Loew's terminology to its original meaning. The first two conditions are not significantly different and we have dropped the term *monolectic*.

TABLE 1. *Known pollen sources for North American species of* Diadasia

Malvaceae				Cactaceae esp. *Opuntia*	Compositae esp. *Helianthus*	Convolvulaceae *Convolvulus*	Onagraceae *Clarkia*
Sphaeralcea	*Callirhoe*	*Sidalcea*	*Sida*				
D. diminuta (Cresson)	*D. afflicta* (Cresson)	*D. nigrifrons* (Cresson)	*D. consociata* Timberlake	*D. australis* (Cresson)	*D. enavata* (Cresson)	*D. bituberculata* (Cresson)	*D. angusticeps* Timberlake
D. laticauda Cockerell				*D. opuntiae* Cockerell			
D. lutzi Cockerell				*D. rinconis* Cockerell			
D. martialis Timberlake							
D. mexicana Timberlake							
D. nitidifrons Cockerell							
D. olivacea (Cresson)							
D. palmarum Timberlake							
D. sphaeralcearum Cockerell							
D. tuberculifrons Timberlake							
D. vallicola Timberlake							

termed oligolecty, and is reflected in physiological and morphological adaptations which sharply limit the number and kind of pollen sources normally utilized by bees with this inherited characteristic.

The general subject of flower constancy has been comprehensively reviewed by Grant (1950) and certain phases have been discussed recently by Michener (1954). The latter author comments on difficulties associated with the definition of the term oligolecty. For purposes of the present discussion oligolectic species may be defined as those in which the individual members of the population, throughout its range and in the presence of other pollen sources, consistently and regularly collect pollen from but a single plant species or from a group of similar or related plant species, turning to other sources, if at all, only when there is a local shortage or absence of that pollen. Such species exhibit physiological adaptations to the host flower such as short flight seasons which are more or less synchronized with the blooming period of the host plants, or sometimes special diurnal flight periods coinciding with unusual times of pollen availability. Also morphological adaptations may exist for the extraction or carrying of the pollen or to facilitate the simultaneous extraction of nectar from the pollen plant.

A substantial number of flower records have been published for species of *Diadasia* (cf. Cockerell, 1898, *et seq.;* Timberlake, 1939, *et seq.*), mostly without distinguishing between pollen and nectar visits. Thus, from a survey of the literature, one might conclude that several of the species of *Diadasia* gather pollen from a variety of plants, but this does not appear to be the case. Michener (1936, 1937) has contributed a number of critical flower records and his catalogue of species (Michener, 1951) is particularly valuable since it includes not only significant records from the literature but reflects first-hand knowledge of the flower relationships of these insects.

Present knowledge of the pollen sources for the North American species of *Diadasia* (table 1) indicates that this genus is composed of species which are oligolec-

tic. The majority of these are associated with plants of the family Malvaceae, mostly with species of the genus *Sphaeralcea.* Presumably these bees evolved in geographic isolation, appropriate conditions for which undoubtedly existed and still exist in the peripheral and isolated mountain ranges of the areas of southwestern United States and northern Mexico where this group of bees is most abundant, as are their host plants (Kearney, 1935). Subsequently, a number of these have spread into the same areas (perhaps since the advent of agriculture and the construction of roads) and now appears to be wholly or partially sympatric and associated with similar or identical pollen sources. If this pattern is to remain relatively stable in terms of the environment, some means presumably will be developed for minimizing the competition for food which results. In andrenid bees of the subgenus *Onagrandrena,* and among certain species of *Ptilandrena* this is accomplished by a partial division of the diurnal period in which the pollen is available (Linsley, MacSwain and Smith, 1955; Linsley and MacSwain, 1956). Our data are not precise enough to reveal whether this situation obtains in *Diadasia,* although, in a locality where two species were taking pollen from the same flowers, we noted that *D. olivacea* seeks nectar at the flowers an hour before the first *D. diminuta* appear, possibly setting the stage for such a development.

In view of the association of most *Diadasia* with Malvaceae, the restriction of *D. enavata* to Compositae, *D. angusticeps* to Onagraceae and *D. bituberculata* to Convolvulaceae, suggests the possibility of sudden and abrupt changes in pollen sources. The first two species exhibit morphological adaptations of the tibial scopa for the gathering and carrying of pollen grains from their respective plant sources (plumose hairs for small pollen grains of the Compositae in the former case, stiff non-plumose hairs in the second case for extracting the spherical pollen grains of Onagraceae, which are bound together by viscin threads. *D. bituberculata,* on the other hand, has elongated, specialized mouthparts suitable for extracting nectar from the deep flower of *Convolvulus,* while simultaneously gathering pollen. A similar specialization occurs in the species of the related genus *Melitoma* which are associated with flowers of *Ipomoea.* Whether these represent subsequent adaptations or perfection of pre-adapted features cannot now be determined. In 1952, on the Borrego Desert of California we found a female of the cactus oligolege, *D. australis californica* taking pollen from *Phacelia,* when pollen from the few locally available blooms of cactus had been exhausted, indicating that this species, at least, will turn to distantly related plants in the face of a local shortage of the usual pollen source. A second female, taken from *Phacelia* flowers at the same time, was not gathering pollen from that plant, yet she had less than a dozen grains of cactus pollen on her body.

It is interesting to note that species now included in the megachilid genus *Lithurge* somewhat parallel the flower relationships of *Diadasia.* The North American species are all associated with Cactaceae (Michener, 1951, 1954). Of the Old World species *L. dentipes* (Smith) collects pollen from *Hibiscus* (Malvaceae), *L. fuscipennis* (Lepeletier) and *L. chrysurus* (Fonsc.) from Compositae (Malyshev, 1930).

In conclusion, we would like to reemphasize that oligolecty is a relative phenomenon. Properly understood, and used with a knowledge of mating habits and certain other biological characteristics it provides explanations for many evolutionary phenomena in the bees. Thus, it may be regarded as a mechanism which permits the survival of large numbers of sympatric species in those groups which have this characteristic (most *Perdita, Andrena,* etc.) by assuring that in years of pollen shortage, competition for that which is available will be among members of the *same* species. In years when the appropriate pollen is completely lacking, the less adaptable species will become locally

extinct, fragmenting the species geographically and the stage may be set for geographic speciation resulting in *closely related allopatric species with the same pollen plant.* With the breakdown of geographical barriers permitting these species to come together the result is a group of *closely related sympatric species with the same pollen plant.* On the other hand, the adaptable species, for example, those without specialized pollen collecting apparatus, or those which are preadapted for another flower, will presumably be able to change their food habits and, if the flowers are the site for mating, isolation can become effective and provide a mechanism for speciation resulting in *closely related sympatric or allopatric species with quite different pollen plants.* In *Diadasia,* available evidence suggests that, at various times in the past, each of these mechanisms may have played important roles in the evolution of species now found in North America. Furthermore, these processes appear to be in active operation today, presumably to produce the new forms of tomorrow.

Summary

At least thirteen of the North American species of *Diadasia* are oligolectic visitors to plants of the family Malvaceae, especially of the genus *Sphaeralcea.* Presumably most of these species evolved in geographic isolation in the peripheral and isolated mountain ranges of southwestern United States and northern Mexico, where the bees and their pollen plants abound, and have subsequently been brought together through the advent of agriculture and man-made roads which favor both. However, three species are oligoleges of *Opuntia* (Cactaceae), one each of *Clarkia* (Onagraceae), *Convolvulus* (Convolvulaceae) and of *Helianthus* (Compositae), suggesting speciation associated with a sudden change of pollen plants. Data derived from a study of one of the cactus-visiting species indicate a possible mechanism by which this might have occurred.

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EVOLUTION IN THREE GENERA OF AUSTRALIAN FROGS

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Introduction

During the past five years the authors have been engaged on a program of study directed towards solving problems relating to speciation processes, breeding behaviour, and ecology in the Western Australian frog fauna. The preliminary work on three genera is now completed but not fully published. As publication of the details will take some time, it was thought advisable to summarize the evolutionary conclusions, which can be presented independently of the biological and taxonomic papers.

Material

The present paper is based on the genera *Crinia* Tschudi, *Heleioporus* Gray and *Neobatrachus* Peters.

Subsequent to the most recent review of the Australian Leptodactylid frogs (Parker, 1940), species have been described in the above genera by Moore (1954), Lee and Main (1955), Main (1957a,b) and Littlejohn (1957), totaling four species of *Crinia,* two species of *Heleioporus* and one species of *Neobatrachus.* The recently described species have been based on the following criteria:

(a) *Crinia:* differences in male call which have been confirmed as characteristic of species populations when genetic incompatibility has been demonstrated by means of *in vitro* crosses (Moore, 1954; Main, 1957; Littlejohn, 1957).

(b) *Heleioporus:* differences in male call, differences in morphology, sympatric occurrence and absence of intermediates even where breeding congresses have as many as four species breeding simultaneously (Lee and Main, 1955).

(c) *Neobatrachus:* criteria as for *Heleioporus.*

The interpretation advanced below to embrace the evolution of species in the three genera was developed initially for *Crinia* and it is proposed to deal with this genus first. However, much of the plausibility of the suggested interpretation derives from its applicability to the three genera.

(a) *Crinia*

Parker (1940) lists ten species in the genus: eight monotypic, one with two subspecies (*C. laevis*), and one with three sub-species (*C. signifera*). Moore (1954) by means of the laboratory technique of *in vitro* crossing demonstrated the absence of genetic isolation between representative of *C. signifera montana* and *C. signifera englishi* and representatives of the eastern Australian population of *C. signifera signifera.* Similar techniques indicated considerable incompatibility between New South Wales and Western Australian representatives of *Crinia signifera.* As Moore (1954: 70) says, "In fact, genetic divergence has reached a point where the two populations should be recognized as separate species." *Crinia signifera* was therefore restricted to southeast Australia and a new name, *C. insignifera* Moore, proposed for the southwest species formerly known as *Crinia signifera.*

Further work reported by Main (1957a) revealed two more species and considerably greater complexity among the species of *Crinia* than had been indicated by Moore (op. cit.). Continuing from Main's work Littlejohn (1957) demonstrated the presence of yet another bio-

TABLE 1. *Summary of species of the genus* Crinia *currently recognized in Australia (1957)*

Western Australia	Eastern Australia
rosea Harrison	*laevis* (Günther)
leai Fletcher	*laevis victoriana* Boulenger
georgiana Tschudi	*actutirostris* Andersson
glauerti Loveridge	*darlingtoni* (Loveridge)
**insignifera* Moore	*haswelli* Fletcher
**pseudinsignifera* Main	*tasmaniensis* (Günther)
**subinsignifera* Littlejohn	**signifera* Girard
	**parinsignifera* Main

* Formerly confused with *C. signifera* Girard.
† Formerly containing three sub-species (*C. signifera signifera* Girard and *C. signifera montana* Parker *C. s. englishi* Parker).

logical species of *Crinia* in Western Australia. The discovery of further species of *Crinia* from South-western Australia is now considered unlikely. The named species recognized at present are listed in table 1.

By the use of biological as distinct from morphological criteria it has been shown that all *Crinia* listed in table 1 which occur in Western Australia are reproductively isolated populations and hence valid species. A similar analysis has only been completed for four eastern species (*C. laevis, C. tasmaniensis, C. signifera* and *C. parinsignifera*). Nevertheless with the addition of the other three morphological species listed which occur in east-

ern Australia we find that the physiographically diverse and ecologically more complex southeast has no more species than the physiographically featureless and ecologically simple southwest. The paradox of a large number of biologically valid species occurring in an area which lacked any sort of geographical barrier prompted closer scrutiny of the *Crinia* complex in order to study possible speciation processes.

All the species of *Crinia* described by Moore (1954), Main (1957a), and Littlejohn (1957) were formerly included within *C. signifera* as understood by Parker (1940). Resolution of the problem of how so many biological species could arise, in the absence of easily visible geographic barriers in Western Australia, led to an investigation of the biology of these frogs in order to see whether special factors other than geographical barriers, operated so as to initiate speciation processes in this group. Needless to say none was revealed.

Main (1957a) using morphology, male call and biology grouped the *signifera*-like crinias into a *signifera* super species with *signifera* in the southeast and *glauerti* in the southwest and an *insignifera* super species with *parinsignifera* in the southeast and *insignifera* and *pseudinsignifera* in the southwest. Subsequently Littlejohn demonstrated that another species (*subinsignifera*) belonged to this group

FIG. 1. Known distribution of species of the *insignifera* and *signifera* species groups in southern Australia: 1. *C. insignifera*, 2. *C. subinsignifera*, 3. *C. glauerti*, 4. *C. pseudinsignifera*, 5. *C. parinsignifera*, 6. *C. signifera*.

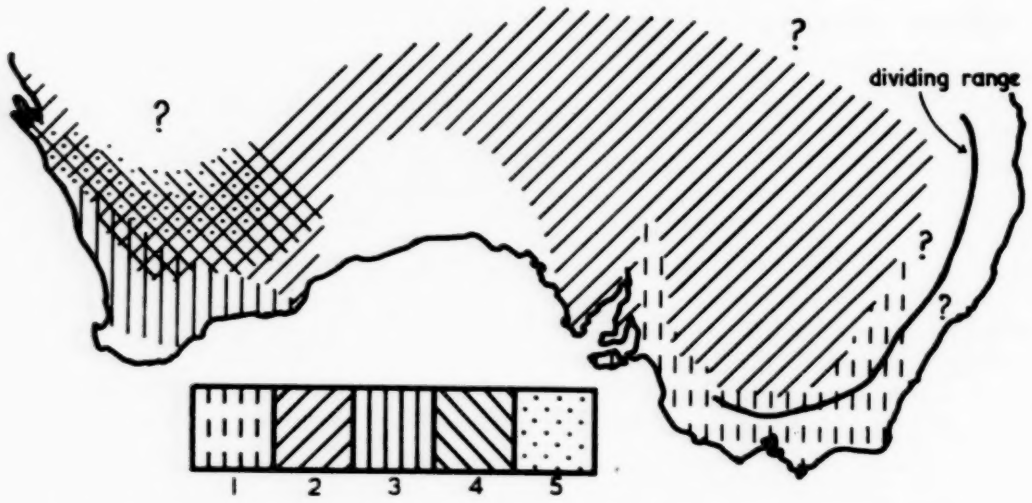

FIG. 2. Known distribution of species of *Neobatrachus:* 1. *N. pictus,* 2. *N. centralis,* 3. *N. pelobatoides,* 4. *N. sutor,* 5. *N. wilsmorei.*

in the southwest. The known distribution of these species is shown in figure 1.

The significant elements in the biology of the two super-species appears to be: (a) the *signifera* group prefer permanent water or at least permanently wet situations and breed throughout the year after rain; (b) the *insignifera* group frequent areas which contain water only during the winter and are dry in summer, and breed only in winter.

In the light of the biology the speciation problem revolves around an analysis of those species presumably adapted to marked seasonal conditions because it is this group which has the greatest number of species. As will be seen later similar problems arise with both *Neobatrachus* and *Heleioporus.*

(b) *Neobatrachus*

The genus *Neobatrachus* Peters has been since Boulenger (1882), synonymised with *Heleioporus* although there are clear morphological differences (Parker, 1940: 33). The observations of Nicholls as reported in Parker (op. cit.: 37) are clearly faulty. All breeding congresses observed by the present authors have been in open water with eggs laid in a long string on the bottom. The morphological and breeding differences suggest that *Neobatrachus* should be revived as a valid genus. Included in the genus are five species: *N. pictus* Peters, *N. pelobatoides* (Werner), *N. centralis* (Parker), *N. wilsmorei* (Parker) and *N. sutor* Main. The distribution of these species as known at present is shown on figure 2.

Parker (1940: 37) recognised *pelobatoides* of the southwest as the analogue of the eastern *pictus,* the former breeds in early winter at air temperatures between 11° and 16° C and on slight evidence it appears that *pictus* is also a winter breeder and spring breeder. On the other hand *centralis* breeds primarily during summer yet small breeding congresses may develop during early winter if rainfall occurs with air temperature higher than 16° C. *N. centralis* is the only species of the genus with a continuous distribution across Australia. The other two species in the genus (*wilsmorei* and *sutor*) are restricted to arid southwestern Australia. Both breed after summer rains when air temperatures are higher than 20° C. Where these last two species occur sympatrically with *centralis* they may all breed in the same ponds following suitable summer rain; however, should the summer rains fail only *centralis* will breed with the first winter rains. Summarising in terms of breeding air temperature preference, *pelobatoides* (11° to 16° C) has a narrow preference at the lower temperatures; *centralis* has

a wide tolerance at moderate to high temperatures (16° to 31° C; while *wilsmorei* 22° C and above, and *sutor,* 20° C to 31° C, have a narrower preference in the upper temperature range. The temperature preferences of these species relate to the geographical distribution; and *N. pelobatoides* is restricted to the wetter portion of the southwest with predominantly winter rainfall while *centralis, wilsmorei,* and *sutor* are found in the more inland areas where there is a marked seasonal incidence of rainfall with a peak in summer.

Heleioporus

The genus *Heleioporus* contains five species, *australiacus* (Shaw), *albopunctatus* Gray, *eyrei* (Gray), *psammophilus* Lee and Main, and *inarnatus* Lee and Main. The distribution of the species of *Heleioporus* is shown in figure 3. *H. australiacus* has an extraordinary fragmented distribution (no doubt these two populations would behave as valid species if biological tests could be applied) but the remaining four species are restricted to southwestern Australia where *H. albopunctatus* and *H. eyrei* have more extensive geographical ranges than the other species.

All species of *Heleioporus* lay eggs in a frothy mass at the bottom of a special burrow, excavated in damp soil by the male early in autumn after rain. Eggs develop into small unpigmented larvae within the frothy mass. Several weeks after egg laying the burrows are flooded by heavy winter rains and the larvae released into the water where they develop to metamorphosis.

Where species occur sympatrically all breed at the same season and show no marked preference for breeding at particular temperatures as do the various species of *Neobatrachus.* However, *albopunctatus, psammophilus,* and *eyrei* all prefer sandy situations while *australiacus* prefers clay soils on hillsides and *inornatus* is restricted to sandy peat bogs. The larvae of the first three species are readily distinguished morphologically from those of *inornatus* and *australiacus* which are so similar morphologically that they can only be identified specifically when the collecting site is known, e.g. *inornatus* larvae remain within the burrow in which the eggs were laid while *australiacus* larvae are found in clear cold torrents in the hills of the Darling Range.

Data are incomplete on the eastern Australian distribution of this genus but *inornatus* and *australiacus* can, on larval morphology, be regarded as a species group in contrast to the *albopunctatus-psammophilus-eyrei* group. A species of this latter group might be expected from inland New South Wales and Victoria

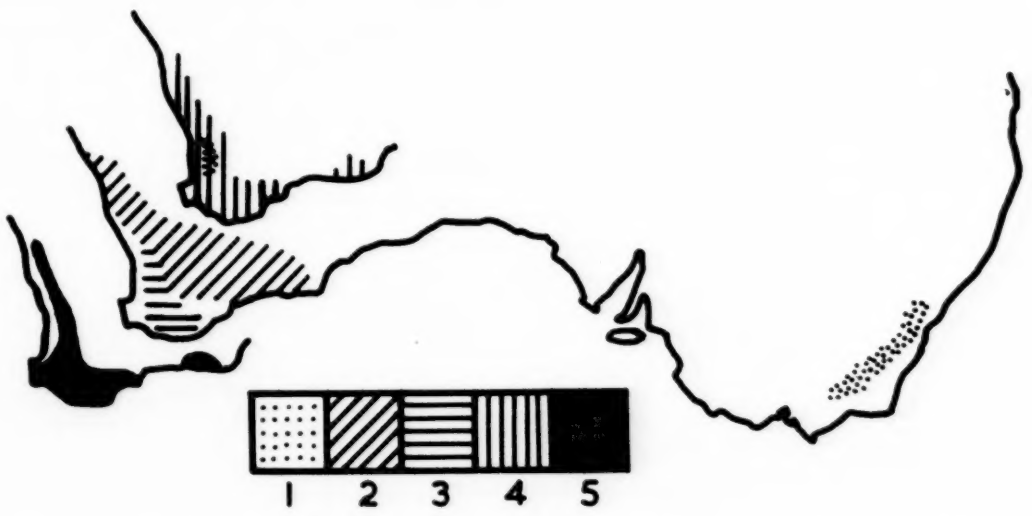

FIG. 3. Known distribution of species of *Heleioporus:* 1. *H. australiacus,* 2. *H. albopunctatus,* 3. *H. psammophilus,* 4. *H. eyrei,* 5. *H. inornatus.*

in the general area occupied by *C. parinsignifera* and *N. centralis*. Should intensive search fail to reveal the presence of such a species at the present time it is postulated, in accordance with the evolutionary explanation tendered below, that such a hypothetical species occupied the inland southeast in the past.

Interpretation

Historical

Before proceeding with an evolutionary interpretation of the material presented above it will be necessary to sketch biogeographical concepts in regard to the faunal and floral relationships within the Australian region.

Tate (1889) extended the work of previous botanists who had noted that the flora of Australia consisted of both an immigrant and an endemic element by dividing the Australian endemic flora into three types, as follows:

1. Euronotian: dominant in the south and east part of the continent.
2. Autochthonian: restricted to the southwest corner of Western Australia (approximately south and west of the dotted line shown in figure 4).
3. Eremean: dominant in the dry central region of the continent.

Spencer (1896) in his summary of the zoological and botanical results of the Horn Expedition points out (p.177), "there is no evidence pointing to the fact that in the case of the most important groups of Australian animals—the Monotremes and Marsupials—the old western part of the continent has any claim to the title Autochthonian." Spencer then summarises the findings of the expedition in regard to all other animal groups collected and after reviewing the probable geological and faunal history concludes that the results of these series of events was the division of the continent into:

1. A northern, eastern and southeastern coastal area which he divided into: (a) the northern part having some elements recently derived from Papua, this area termed the Torresian sub-region. (b) the southern part of this coastal strip lacked a dominant Papuan faunal element and was termed the Bassian sub-region.
2. A large central, western and southern area comprising the rest of the continent not included in 1 above; this he termed the Eyrean sub-region.

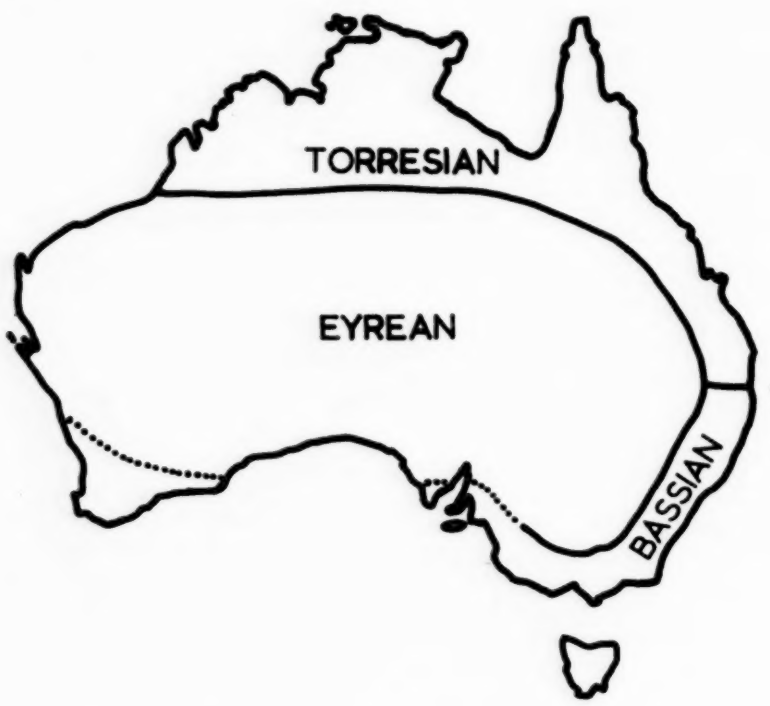

Fig. 4. Zoogeographic regions of Australia.

The distribution of these provinces is shown in figure 4.

Nicholls (1933) after an exhaustive literature review concludes that the south-west of Australia should be recognised as a biogeographic province but objected to the implications of the term Autochthonian and proposed the term Hesperonotian for the region lying west and south of the dotted line shown in figure 4. This, however, has not found favour as zoologists, especially ornithologists who while appreciating the validity of the faunal boundary realized that faunal elements rather than static faunal provinces ought to be recognised. Serventy and Whittell (1951, p.46) modified Spencer's terminoloy and spoke of Bassian and Eyrian faunas. Serventy and Whittell note that the southwest (i.e. Nicholls Hesperonotian region) contains both Eyrian and true Bassian elements and speculate as to which is the "true autochthonian."

As knowledge of Western Australian frogs increased an attempt was made to match the species with the named provinces to see whether this assisted in an evolutionary interpretation. The success of this attempt is reported below:

Geographical

The initial boundary between the Bassian and Eyrean region in southeastern Australia is the Great Dividing Range. In Late Tertiary, probably Pliocene times, these mountains may be envisaged as isolating the fauna of southeastern Australia into an inland (Eyrean) and a coastal (Bassian) component. In geographical isolation these divided populations reached species status and became adapted to the characteristic habitats present which, in turn, were determined by the seasonal (Eyrean) and non-seasonal (Bassian) nature of the rainfall. In terms of climate the Bassian subregion has a uniform rainfall while the Eyrean contains a variety of climatic types all of which have a markedly seasonal rainfall.

In eastern Australia the distribution of species tends to follow the boundaries of Spencer's provinces and it is possible to classify the frogs of the southeast into Bassian and Eyrian species merely by knowing their geographical range. Because of the marked climatic differences between the two regions one is not surprised to find equally distinctive differences in the ecology of related Bassian and Eyrean frogs. By use of the knowledge gained from studying breeding and ecology of the eastern frogs it is possible to identify Bassian and Eyrian elements in the frog fauna of southwestern Australia.

The breeding biology of *C. signifera* and *C. glauerti* typifies what would be expected of a Bassian species. On the basis of distribution, breeding season, and cooler temperatures preferred for breeding, both *N. pelobatoides* and *N. pictus* may also be classified as Bassian species. Finally *H. australiacus* has a Bassian distribution and the similar morphology of the larvae of this species and *inornatus* along with the peculiar type of larval habitat indicates that the two should both be grouped together as Bassian species. On the basis of distribution and ecology the other three species of *Heleioporus* discussed earlier are considered as being Eyrean.

Moore (1954 : 73) suggests that the presence of *C. tasmaniensis* and *C. signifera* in Tasmania indicated the possibility of a double invasion of the island of Tasmania. It seems plausible to account for the species present in southwestern Australia by postulating an analogous series of repeated invasions from the primary speciation area in southeastern Australia (Bassian and Eyrean). These repeated invasions took place as the climates changed throughout the Pleistocene. In favourable times both Eyrean and Bassian forms invaded the southwest. In times of marked seasonal rainfall, however, not only was the west

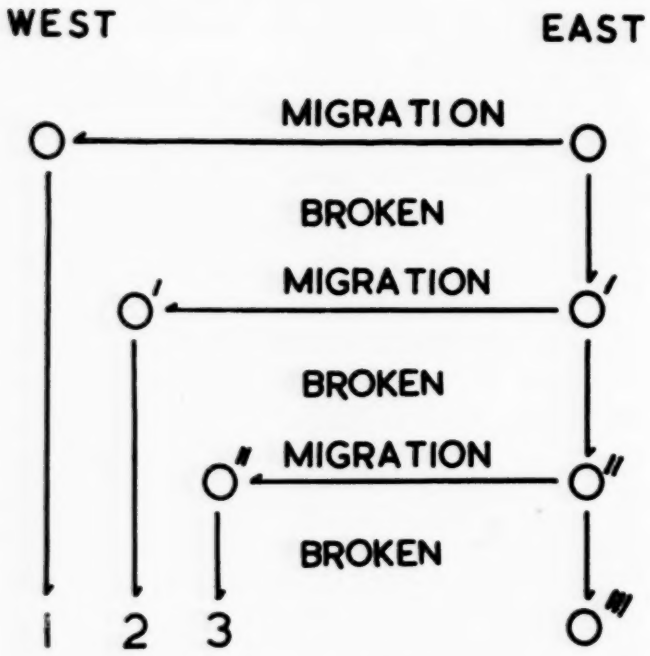

FIG. 5. Diagrammatic representation of hypothetical east to west migration followed by speciation (1, 2, 3) in Western Australia. The symbols O, O′, O″, O‴ represent the one ancestral population which has persisted through time. 1, 2, 3 represent the species which may be found at present in Western Australia.

isolated from the east by a desert but in both *Crinia* and *Neobatrachus* all traces of earlier Bassian invaders were erased, so that at the present time only the most recent Bassian invader occurs. On the other hand, in *Heleioporus* both the last Bassian (*australiacus*) and the penultimate invader (*inornatus*) survive. However, in the Eyrean species earlier invasions were not erased by climatic deterioration and in each genus there are three populations, now species, each representing an earlier invasion. The process can be represented as in figure 5.

The order in which the invaders arrived can be established by using a combination of the following:

(a) The most recent migrant is indicated:
   i. Where the east-west distribution is unbroken, e.g. *N. centralis.*
   ii. Where the east-west distribution is broken but morphological differences are absent, e.g. *H. australiacus.*
   iii. Where the east-west distribution is broken but eastern and western populations can, on morphological evidence, be recognised as being more closely related to each other than to other eastern or western populations, e.g. *N. pelobatoides* and *N. pictus.*
   iv. Where the east-west distribution is broken but eastern and western populations can be arranged for closeness of relationship on similarity of male call and genetic closeness demonstrated by laboratory hybridisation experiments, e.g. species of the genus *Crinia;* those with least hybrid inviability and most similar male calls are most recent.

(b) The order of arrival of earlier migrants is indicated as follows:
   i. Those most similar in morphology to the last invader are the penultimate migrants and those least similar are the first migrants.
   ii. Greatest distinctness in male call and most marked hybrid inviability indicates earlier migrants, the penultimate migrant is intermediate between the first and last invader in these characteristics.

In figure 5 the symbols O, O′, O″, O‴ represent the ancestral population which has persisted through time; 1,2,3 represent the earliest, middle and most recently derived western populations which were separated from the ancestral stock at different times in the past as discussed above. By representing Bassian and Eyrean species by B and E respectively and determining earlier and more recent invaders by the criteria described above it is possible to equate the species discussed in earlier sections with the symbolism represented in figure 5. Thus in *Crinia* EO‴ = *C. parinsignifera;* E_1 *C. pseudinsignifera;* E_2 = *C. insignifera,* and E_3 = *C. subinsignifera;* BO‴ = *C. signifera;* only B_3 persists in the southwest, this = *C. glauerti.* In *Heleioporus* EO has not been found but E_1 = *H. albopunctata;* E_2 = *H. psammophilus,* and E_3 = *H. eyrei. Heleioporus* is the only genus with two Bassian elements in the southwest; those are B_2 = *H. inornatus* and B_3 = *H. australiacus. Neobatrachus* shows yet another variation and the Eyrean elements of the third migration are continuous between east and west; thus *N. centralis* represents EO‴ in the east and E_3 in

the west. E_1 = *N. wilsmorei,* E_2 = *N. sutor*. The Bassian elements are closely similar to *Crinia* and *N. pictus* = BO‴ and *N. pelobatoides* = B_3.

A pattern such as that outlined envisages the main climatic differences between Eyrean and Bassian conditions as being related to cool rather uniform rainfall in the latter when compared with a hotter more marked seasonal rainfall for the former. It follows also that the east-west connection with relatively uniform climatic conditions would be open for Bassian form, while the connection would be broken as soon as contrasting seasonal conditions arose. It seems probable that when the Bassian corridor was open along the south coast the inner fringe was subject to markedly seasonal and irregular rainfall at lower temperatures than those to which the earlier Western Eyrean invaders had become adapted. Thus eastern Eyrean forms could migrate westward, but none could migrate west to east.

N. wilsmorei and *sutor* which are believed to represent invasions E_1 and E_2 are both, in respect to breeding, narrow preference warm temperature species while *centralis,* the E_3 invader, has a wide temperature preference for breeding. Reasoning from this it follows that in the inter-migratory phases seasonal conditions were more intense in western Australia than in eastern Australia, that is to say, migration to the west was possible because eastern climatic conditions extended westward into a region which had just been through a period of most intense seasonal climate. Under cooler more uniform conditions the E_1 and E_2 invaders would be at a disadvantage, and at such times *N. wilsmorei* and *sutor* would, rather than migrating eastward, move north into a region where warm summer rains and marked seasonal conditions provided a habitat similar to that to which they had become adapted during the previous interpluvial.

Reasons for the failure of the earlier *Crinia* and *Heleioporus* migrants (E_1 E_2) to migrate eastwards are not so clear, mainly because the unique elements in the biology are more difficult to detect than in *Neobatrachus*. Both *Crina* and *Heleioporus* species are winter breeders and *C. pseudinsignifera* (E_1) especially requires peculiar conditions for breeding and larval life, viz. breeding congresses only form on very cold nights (air temperature about 6° C) while the larvae require warm water above 25° C for development. These two requirements appear to conflct but cloudless skies are common in mid-winter (July, July) in the range of *C. pseudinsignifera* and with such conditions the nights are cold and the days warm and sunny. During Pleistocene time cloudless conditions would only be possible away from the maritime and presumably cloudy areas associated with an east-west corridor. Our own experience indicates that even the lightest cloud keeps night temperatures sufficiently high to prevent the development of breeding congresses even when other conditions are fulfilled. *H. albopunctatus* (E_1) does not appear to require specific breeding conditions but the larvae appear to require warm water similar to *C. pseudinsignifera*.

At present it is not possible to state categorically whether similar factors could have prevented the counter migration of the E_2 faunal elements but it seems probable that such factors did operate.

H. inornatus is assumed to be the only B_2 invader to survive the last complete seasonal change. This could have been due to the fact that small peat bogs in the far southwest could continue even under seasonal climates because some poorly drained areas having relatively large catchments would collect enough run-off even through the period of stress.

Discussion

The foregoing interpretation poses a number of questions of which the most significant appear to be:

(a) is the pattern of repeated migrations shown in groups other than frogs?

(b) are these repeated migrations to be equated with the major advances of the glaciers in Pleistocene times?

(c) does the identification in the fauna of younger and older migrants allow us to say which are the "true autochthonian elements in the fauna" (Serventy & Whittell, 1951: 49 and Ratcliffe and Calaby, 1954: 179).

In connection with (a) above it is not proposed at present to make a survey of the literature on other groups but it seems that it would be profitable to apply the foregoing as a working hypothesis in the study of the speciation and biology of groups other than birds which Serventy (1951, 1953) and Serventy & Whittell (1951) have already analysed. The work on the genus *Crinia* (Main, 1957) shows quite clearly how little morphological divergence there may be between various migratory components from the one stock separated by a time sequence; without criteria relating to genetic and reproductive behaviour these components would pass unrecognised. It is unlikely that all groups will show a similar speciation pattern and should any fail to fit a study of the biology of the group in relationship to general climatic conditions is likely to produce new evidence of the speciation patterns of the various faunal components.

With regard to (b) above, if the corridor from the east was open during times of glacial advance four migrations to the west might be expected (one each for the Gunz, Mindel, Riss and Würm) each being separated by arid phases corresponding to the Gunz/Mindel, Mindel/Riss and Riss/Würm interglacials and the post-Würm glacial recession. So we should expect four species, one corresonding to each glacial phase. However, only three have been identified.

This non-correspondence may be due to:

1. The three pluvials postulated correspond only with wet stages associated with the Würm glaciation. This interpretation assumes that any faunal migrations during pluvial phases associated with earlier glacial stages of the Pleistocene were extinct by the beginning of Würm time. However, all species in the three genera are well differentiated on breeding biology and it seems unlikely, because of the short time involved, that the degree of speciation observed could have taken place during the stages of the Würm glaciation.

2. Only three glacials and three distinct pluvials occurred in southern Australia; or if there were four then one interpluvial was very short or failed to develop a marked seasonal weather pattern and so connection to the east persisted.

3. There were four pluvials corresponding to the major glacial epochs recognised in the Northern Hemisphere but due to the intensity of the seasonal aridity during one interpluvial an early migrant phase has not persisted in the frogs.

This latter may well be confirmed by study in other groups and it is interesting that Dr. B. Y. Main from work on trapdoor spiders (unpublished data) identifies 5 levels within this group; however, it is possible that at least one of these represents a pre-Pleistocene element, i.e. the "true autochthonian element" listed under (c) above.

If autochthonian is construed to mean an indigenous animal or plant, i.e. an original occupant of the country, it follows from the reasoning developed above in relation to successive migrations that neither Eyrean nor Bassian elements can be strictly said to be autochthonian in southwestern Australia. However, faunal elements which show no generic affinity with eastern Australia may reasonably be said to be indigenous and in the frogs there are two species, viz. *Myobatrachus gouldii* Gray and *Metacrinia nichollsi* (Harrison), which satisfy the above definition of autochthonian. If these highly specialised frogs are an ancient persistent element in the western frog fauna it tends to discount the possibility, discussed under 3 above, that one interpluvial was

so intense that both Bassian and Eyrean faunal elements became extinct.

With regard to the foregoing it may be noted that in southeastern Australia and Tasmania there is evidence of three Pleistocene glacial stages which David and Brown (1950) refer provisionally to the Mindel, Riss and Würm stages respectively. It is reasonable to assume that each glacial stage was associated with a pluvial stage and thus the glacial and biological evidence would agree in suggesting that southern Australia was subjected to three pluvial phases during Pleistocene time as discussed under 2 above.

Summary

1. For a topographically featureless area lacking easily detected geographical barriers Western Australia has an unexpectedly large number of species of frogs in the genera *Crinia*, *Heleioporus* and *Neobatrachus*.

2. The origin of these species is reconciled with current evolutinary theory relating to the origin of species by postulating:

(a) A primary speciation pattern across the Great Dividing Range in eastern Australia. In this manner originated a series of species pairs one of which, the Bassian, was coastal, adapted to a uniform climate, and the other, the Eyrean, was central and adapted to a markedly seasonal climate.

(b) That during Pleistocene time three pluvials, separated by interpluvials, allowed three migrations of the Bassian and Eyrean faunal elements into western Australia.

(c) That during the seasonally arid inter-pluvials the earlier Bassian migrants were lost so that at the present time only the last migration is completely represented; however, each of the earlier Eyrian migratory elements has persisted.

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CHROMOSOMAL ADAPTIVE POLYMORPHISM IN *DROSOPHILA PERSIMILIS* II. EFFECTS OF POPULATION CAGE CONDITIONS ON LIFE CYCLE COMPONENTS[1]

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In the widely studied cases of chromosomal adaptive polymorphism in Drosophila (da Cunha, 1955) a vast inadequacy exists in our knowledge of the adaptive phenotypes which these chromosomal arrangements control. Population cage technique has proved a useful tool in establishing relative adaptive values for two or more chromosomal markers competing under "constant laboratory conditions." It has been shown (Dobzhansky, 1957) that chromosomal arrangements coexisting in wild habitats possess constant adaptive values for specific laboratory environments; it is undoubtedly true that selective forces in nature have built up particular gene complexes in such arrangements, but the phenotypes controlled by these complexes and the selective forces at work in maintaining them remain in large measure to be demonstrated.

In population cages containing Whitney and Klamath arrangements of chromosome III of *Drosophia persimilis,* Spiess (1957a) has shown the former to be adaptively superior to the latter after many generations of coexistence. Spiess and Schuellein (1956) tested certain life cycle components of these arrangements for adaptive differences by using conditions which were rigidly controlled (constant temperature, sterility, low larval density, equal volume of food in replications, and so on). Under these "near-optimal" conditions marked differences in such traits as hatchability of eggs, net survival, and rate of development were demonstrated between karyotype combinations of the arrangements. The net adaptive values for the karyotype combinations calculated from these life-cycle data approximated adaptive values calculated from cage data. If life-cycle components were redetermined under conditions closer to those conditions prevailing in a population cage, the adaptive values might be closer to those obtained from cage frequency data, provided the principal adaptive differences between karyotypes are discovered and utilized for the computation.

The WT and KL arrangements of chromosome III display adaptive differences in experimental populations which are constant; consequently these arrangements should exhibit the same differences from one food cup to another in the population cage. In a population cage it is not usually practicable to control precisely such factors as yeast growth from food cup to food cup, growth of bacteria, molds, and related organisms, humidity, variation in consistency of food medium, and so on. If adaptive phenotypic differences can be demonstrated for these chromosomal variants and their karyotype combinations in spite of environmental variance contributed by food cup conditions, we shall be on more reliable ground in attempting to decide the specific nature of the adaptive phenotypes which these chromosomal arrangements control. By allowing considerable variability in culture conditions during life-cycle component testing, any adaptive properties which remain distinct throughout that range of conditions will be more likely to

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remain distinct under such microenvironmental variation as must exist in the wild habitat of these flies; and perhaps a clue may be given us in solving the problem of the selection mechanism which operates on these chromosomal variants in nature.

With this reasoning in mind, we tested certain adaptive properties of these chromosomal arrangements under conditions which simulated the population cage using exactly the same strains of flies which had been used to test life cycle components under "near-optimal conditions." The objective was threefold: 1) a comparison to see if increase in density altered the net fitness values, 2) a search for adaptive properties which might be characteristic of one arrangement in contrast with the other under more variable conditions, and 3) a reexamination of the net fitness components for each gene arrangement for reference to relative fitness values obtained in the population cage.

Materials and Methods

The three strains of WT and four strains of KL used in these experiments were identical with those introduced into population cages (Spiess, 1957) and with those used to test life cycle components under "near-optimal' conditions (Spiess and Schuellein, 1956). The plan of mating flies as given in the latter reference was preserved exactly in this set of experiments. All flies tested were produced as follows: Stock parents were mated in several replicate bottles about six to ten pairs per bottle and provided with yeasted food on plastic spoons. Eggs were collected daily and planted in lots of ten on the surface of slanted food in glass vials (9.5 X 2 cm.). The volume of food was aproximately the same as that used in a population cage food cup but the food surface area was about twice that of a cage cup. The extra surface was essential for egg planting in order to insure spacing egg lots so that the needle would not accidentally injure eggs already planted on the food surface. At high egg densities, great care had to be taken to avoid disturbing planted eggs when the surface was nearly covered. When larvae reached the second instar, a piece of paper towelling was inserted into the food (paper towelling is also used in population cage food cups); and the vial with cotton stopper removed was placed in a rectangular half-pint bottle which was in turn plugged. Housing the vial in this extra container was necessary to prevent loss of larvae which become entangled in or penetrate through the vial's cotton stopper.

In order to study the effects of increasing density on survival (viability) and on rate of development eggs were planted in the following densities: 50, 100, 200, 300, and 500 eggs per vial. For each strain cross at least three replicates of each egg density were made to obtain a measure of environmental variance. In the population cage most food cups have a very large number of larvae. Nevertheless some variation will exist in numbers from cup to cup. Not only is it important to see how variation in density may affect the karyotypes' survival values, but also it is useful to find some relationships between numbers present and survival or rate of development which might be extrapolated without too great error to actual population cage conditions.

Any yeast, bacteria, or other microorganisms present on the spoons of the mating bottle were automatically transferred to the vial in egg planting. In population cages food cups are supplied with about 5 cc. of thick yeast suspension; food cups often show mold and bacteria colonies. (Note should be made here of an especially obnoxious contaminant, an oxidative yeast, *Pichia membranaefaciens*, identified by Dr. Herman Phaff, which grew faster than *Saccharomyces cereviseae*, and which covered the entire food surface in two days' time with a thick wrinkled scum which noticeably reduced survival of larvae in cultures.)

TABLE 1. *Fecundity of ♀ ♀ in mean eggs/day/ ♀ and components of variance*

Karyotype	Mean	N	Between vials df	Between vials V	Between crosses df	Between crosses V	Between vials within crosses df	Between vials within crosses V	Error df	Error V
WT_1/WT_2	18.86	88	8	17.65	2	26.24**	6	14.79*	79	4.98
KL_1/KL_2	19.74	115	11	36.32	3	1.07	8	49.54**	103	5.70
WT/KL (from WT×KL)	21.15	89	8	54.17	2	41.30**	6	58.46**	80	6.84

* Variance significant at 5% level by F test.
** Variance significant at 1% level by F test.
N = total tested; df = degrees of freedom; V = variance.

Food was made according to the cream of wheat–molasses formula of Spassky (1943) except that the mold preventive was only 10% of that specified. (Tegosept M depresses rate of development at the concentration used in Spassky's formula (see Spiess, 1957b) and all population cage food cups as well as vials in this experiment were given only a minimum of this mold preventive.) The temperature was 16° C.

RESULTS

Egg-laying capacity. It was found in a pilot experiment that females raised under "crowded" conditions were not significantly different in egg-laying capacity from females raised under "near-optimal" conditions. Nevertheless it was important to complete the more extensive experiment reported herein to obtain the best estimate of fecundity for females raised under "population cage" conditions and to measure genetic uniformity and norm of reaction to microenvironmental variation on the part of each karyotype combination by variance analysis.

In view of the pilot experiment's results it was not important to obtain data on fecundity from females raised at all egg densities; therefore only 500 egg density vials were used to raise the females to be tested. F_1 eggs were planted in three "500" vials per strain cross. Adult F_1 females emerging from these "500" vials were isolated and ten were chosen at random from each vial, so that for each strain cross there were initially thirty females to be tested. They were mated singly to sib males in glass vials, one pair per vial, and provided with spoons containing food for egg-counting (See Spiess and Schuellein, 1956, for technique).

The thirty day average fecundities of females according to karyotype together with variance components for each karyotype are given in Table 1. Genetic variance may be represented by variance between strain crosses; environmental variance by that between vials within crosses. It is interesting how closely the mean eggs/day for females raised under these conditions correspond with those for females raised under near-optimal conditions. For comparison the latter data are as follows: WT/WT 18.46, KL/KL 18.40, and WT/KL 20.08 (Spiess and Schuellein, 1956). Apparently average fecundity is not significantly altered by the conditions under which females develop at least within the limits of crowding used. But more significant perhaps is the consistently higher value for the heterokaryotype in both sets of data. The author is indebted to Dr. C. C. Li for his advice in the use of the variance test to find how significantly the homokaryotype and heterokaryotype fecundities may differ for these data from "500" vials. From Table 1 it is evident that the vast bulk of variance comes from genetic and environmental factors; the differ-

ence between karyotype fecundities must be tested by the between vials variance rather than by the error variance. The error variances of table 1 represent the average variance for each ten females per "500" vial. Since the ten females within a vial are quite uniform, the average of the ten from each vial can be dealt with as a unit, and a second variance analysis can be run on the thirty vial averages comprising all three karyotypes. This second variance analysis employed the orthogonal method for calculating sums of squares for the two relevant components of the between crosses variance, and the results are given in table 2.

From table 2 it can be seen that WT/WT and KL/KL do not differ significantly (their variance is less than error). On the other hand the variance contributed by differences between homokaryotypes and the heterokaryotype gives an F value which is slightly less than the 5% level F. If these results alone were the only data available, they would be conventionally relegated to the category of non-significance; however the near-optimal data given in the above paragraph parallel these mean values so remarkably that it is tempting to say there is a slight heterotic effect in the heterokaryotype amounting to about two eggs per day per female over the homokaryotypes which are in turn approximately equal in fecundity. There is no lowering of variance in either the genetic or environmental components in the heterokaryotype, however. This heterotic effect then cannot be said to show "buffering" in the sense of Lerner (1954).

When the remarkable similarity between these "population cage" condition data and the earlier "near-optimal" data are noted, we are faced with the paradoxical high environmental components of variance in table 1. These variances must be produced by environmental factors other than the mere density of larval population, namely by factors such as consistency of food, moisture condi-

TABLE 2. *Variance analysis on egg-laying capacity averages from 30 "500" vials (9 WT/WT, 12 KL/KL, 9 WT/KL) comprising ten strain crosses of three vials per cross*

Source	df	Sum of sq.	Mean sq.	F
WT/WT crosses	2	5.08	2.54	
KL/KL crosses	3	0.51	0.17	
WT/KL crosses	2	9.63	4.81	
*WT vs. KL	1	3.94	3.94	
*Hetero. vs. homokar.	1	20.16	20.16	3.94
Between crosses (subtotal)	9	39.32	4.37	
Within crosses (between vials)	20	102.37	5.12	

* Sums of squares were calculated by orthogonal contrast method below; n = no. of vials.
At p = 0.05 level; df = 1,20; F = 4.35. The comparison between heterokaryotype and homokaryotypes is just short of statistical significance.

	(3) WT/WT	(4) KL/KL	(3) WT/KL	Z	Z^2	D	Z^2/D = s.sq.
Σ =	169.8	236.9	190.4				
n =	9	12	9				
ortho. coef. (1)	−4	3	0	31.5	992.25	252	3.94
(2)	−3	−3	7	112.7	12701.29	630	20.16

TABLE 3. *Average per cent survival under varying population densities (number of adults emerging per eggs planted in a vial)*

	Egg densities									
	50		100		200		300		500	
Karyotype	N	%	N	%	N	%	N	%	N	%
WT_1/WT_2	19	36.13	19	38.50	19	45.47	12	45.73	9	36.37
KL_1/KL_2	21	49.52	12	50.40	12	48.40	13	39.45	12	37.47
WT/KL	11	48.60	9	48.00	13	43.93	8	53.60	9	41.11

N = Number of vial cultures.

tions, presence of microorganism contaminants, availabilty of yeast and so on. In population cage food cups density of larvae must be much greater than in "500" vials, but there is no reason to assume that fecundity of females in cages should be significantly affected by that increase though individual food cups may produce widely variable conditions. There is no significant correlation in these experiments between fecundity and number of survivors in a culture. Correlation coefficients (r) of mean eggs per day on survivors are as follows: for WT/WT, $r = -0.477$ (d.f. = 7, 5% level $r = -0.66$), KL/KL, $r = 0.093$ (d.f. = 10, 5% level $r = 0.576$); WT/KL, $r = -0.478$ (d.f. = 7). None of these values are significant; therefore under the conditions of crowding in this experiment, the density of preadult stages is not by itself sufficient to account for the high environmental component of variance in fecundity of adult females.

Percent survival and increasing density. The average percentage of adults emerging per eggs planted in a vial is given in table 3. The most striking fact from these data is the lack of effect increasing density has on survival. Apparently these flies have a nearly constant average viability irrespective of the larval or egg density within the limits tested. At the same time the survival values are about half those for flies raised under near-optimal conditions, which for the sake of comparison were as follows: WT/WT 84.6%, KL/KL 80.8%, and WT/KL 89.4%. The difference between the values obtained under population cage conditions and near-optimal conditions cannot be accounted for on the

TABLE 4. *Variance analysis on survival data from "500" vials*

Source	df	Sum of sq.	Mean sq.	F
WT/WT crosses	2	8982	4491	1.39
KL/KL crosses	3	49827	16609	5.16**
WT/KL crosses	2	23478	11739	3.65*
***WT/WT vs. KL/KL	1	163	163	<1
***WT/KL vs. WT/KL	1	2662	2662	<1
Between crosses (subtotal)	9	85112	9457	
Within crosses	20	64408	3220	
Total	29	149520		

*** Sums of squares were calculated by orthogonal contrast method as in table 2.
* F = 3.49 at 0.05 level.
** F = 4.94 at 0.01 level.

basis of increasing concentration of flies alone: increasing egg density has no significant effect on reducing the proportion of survivors. The impression is that a constant survival value is the result of a constant egg-hatchability and larval-pupal mortality which are not affected significantly by increases in population density. If these factors are lower under population cage conditions the introduction of bacterial and mold contaminants, increased moisture conditions, and decrease of food surface available might be responsible in some degree. Which of these factors may be responsible it is not possible to say, though the most likely would be bacterial contaminants.

In Table 4 a variance analysis on the survival averages from "500" vials shows that no components of variance between homokaryotypes or between homo- and heterokaryotypes are significant; the latter component is about sixteen times greater than the former, but the error variance (within crosses) is so large that this difference between WT/KL and the homokaryotypes is concealed. Obviously survival may be very high or very low depending upon specific conditions of a vial, though the low average survival indicates a high average contamination for all the vials, and no karyotype has any significant resistance to the adversity of conditions distinguishing it from other karyotypes. Nevertheless it is again interesting to note the parallel between survival at near-optimal conditions compared with survival in "300" and "500" vials: in both cases the heterokaryotype has highest average survival and by about the same magnitude difference from homokaryotypes. This apparent superiority of WT/KL may be real for cultures in which microorganism contaminants can be held in check as in sterile near-optimal cultures and in the high density cultures described here where there are sufficiently large numbers of larvae consuming microorganisms.

From table 4 it is obvious that the greatest variance in survival is contributed by specific strain cross differences, especially in the two karyotype combinations containing the KL arrangement. It may be concluded that specific survivorship of any F_1 is controlled by the total genotype rather than by genotypes particular to the arrangements of chromosome III. This conclusion was also reached by Spiess and Schuellein (1956) on the basis of comparing parental strain eclosion with strain cross F_1 eclosion. That is, while the heterokaryotype is slightly superior in survival to the homokaryotypes under both near-optimal and population cage conditions, the greater amount of genetic control of viability is contributed by specific genetic combinations brought about in particular F_1's, and the karyotype per se is relatively ineffective in such genetic control.

Rates of development. Records of emergence were kept every two days from the date of emergence of the first fly in any vial until flies ceased to emerge in that vial. The mean time for preadult development in number of days was computed by weighing the number of days by the number of flies emerging on any date. The rate of emergence does not follow a "normal distribution" but is slightly skewed; most flies emerge early and the last ten percent may linger with only one or two flies emerging per day. The mode of development time would be possibly a more realistic measure than the weighted mean time, but it is far less economical to calculate.

Duration of preadult stages in Drosophila is dependent to a large extent upon the number of individuals in the culture and ultimately upon the availability of yeast (Sang, 1949). A useful method of describing the rate of development, then, is by a regression of mean days (from egg to adult) on survivors in a culture. Correlation and regression coefficients with standard errors of estimate are given in table 5. A scatter diagram of the regressions for each karyotype is given in figure 1.

Of the three karyotypes, WT/WT de-

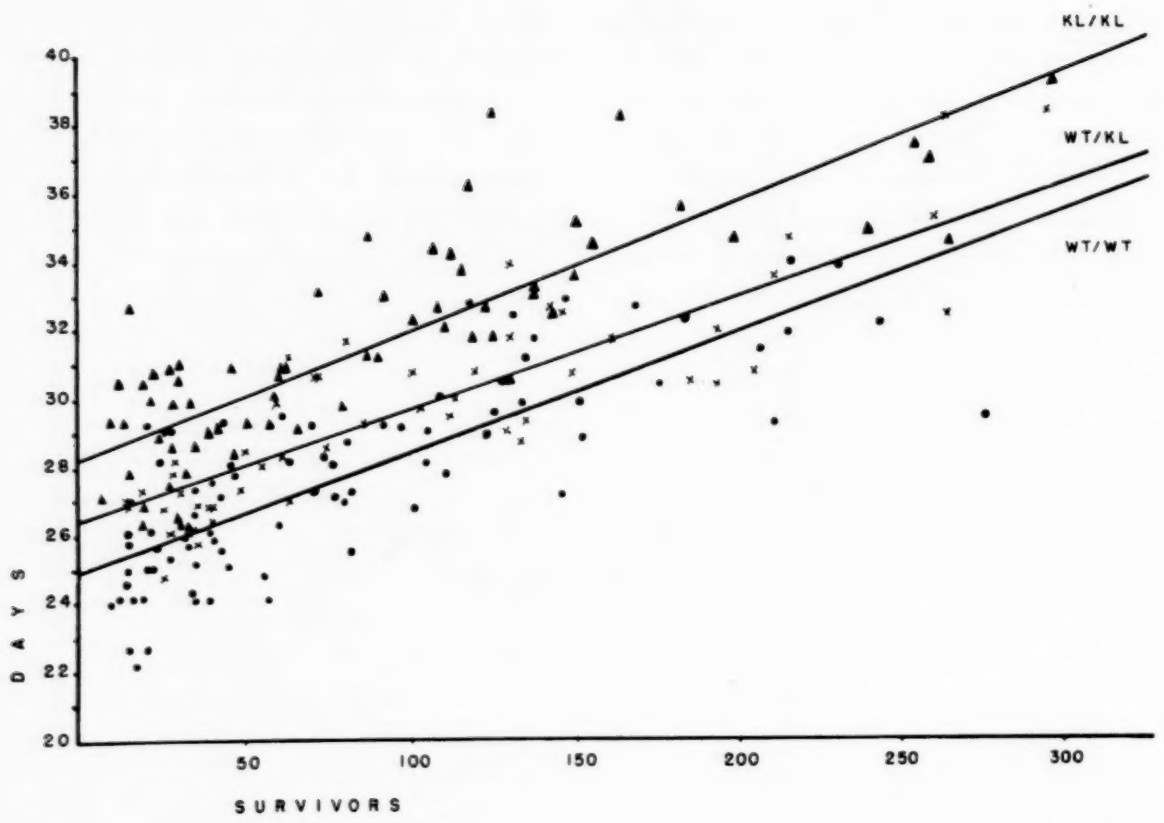

FIG. 1. Scatter diagram and average regressions for three karyotypes of days (preadult development time) on survivors in a culture. Triangles = KL/KL; crosses = WT/KL; and dots = WT/WT.

velops most rapidly, KL/KL takes more than three days longer, while WT/KL is intermediate in length of development (see table 5, the "a" coefficient, or the number of days for a single individual's preadult development). Though the heterokaryotype has the most gentle slope (b = 0.034), KL/KL the most steep (b = 0.0389), they are not very far from parallel so that under these conditions it would appear that differences in time of development for low density cultures would be nearly equal to differences among high density cultures. In other words KL/KL is uniformly a slow developer, WT/WT is consistently fast, and WT/KL intermediate irrespective of the density of the culture.

TABLE 5. *Correlation and regression between average days (egg to adult) and the number of survivors in a culture*

Karyotype	N	r	a (Days)	b (Slope)	σ_{est}
WT_1/WT_2	82	0.801	24.90	0.0360	1.723
KL_1/KL_2	72	0.831	28.22	0.0389	1.796
WT/KL	51	0.872	26.42	0.0334	1.291

N = no. of vial cultures, r = average correlation within crosses, a and b = regression coefficients of days on survivors, σ_{est} = regression standard error of estimate.

Covariance analysis was run on the WT × WT, KL × KL, and WT × KL crosses separately; for each karyotype the differences among cross regressions were less than error, so that each karyotype's results were averaged (see Snedecor, 1946, pp. 325–328 for the method used in averaging these regressions).

Under near-optimal conditions the discrepancies between karyotypes were more marked, but KL/KL again was slowest, while WT/KL was fastest with WT/WT nearly equal to WT/KL. One principal phenotypic difference which these genetic complexes may control is rate of development. At least under the wide variety of microenvironments possible in population cage conditions rate of development remains distinctly measurable with very

little overlap between the two homokaryotypes concerned.

Because this fact seems so crucial to this study, the "500" vials of four homokaryotype and three heterokaryotype crosses were retested simultaneously six months after the original tests had been completed. These repeat results were as follows:

WT/WT with 159 (average) survivors took 29.6 days.

KL/KL with 187 (average) survivors took 34.4 days.

WT/KL { (1) with 141 (average) survivors took 32.1 days. (2) with 239 survivors took 34.1 days.

These rate of development differences seem significant and repeatable. They fit the regression lines already calculated (see figure 1) quite well, and confirm the fact that these karyotypes differ in rate of development.

Rates of maturation. With the fact in mind that flies native to high elevation possess a chromosomal polymorphism which controls rate of preadult development, the question arises if this rate control extends to rate of maturation of adults (the time required from eclosion to oviposition). Females from the repeat experiment above (from "500" vials) were isolated and mated to their sibs in separate vials, one pair per vial, and spoons were checked every day for eggs. The number of days between the day of female eclosion and the first day of egg-laying was considered the rate of maturation. The averages of the three karyotypes for a minimum ninety females per karyotype tested are as follows:

WT/WT = 6.31 days; WT/KL = 6.16 days; and KL/KL = 6.07 days. It is obvious that maturation rates of the three karyotypes are very nearly equal. Rate control seems confined then to the post-embryonic stages of development, and from the previous work on near-optimal conditions this control seems largely to occur in the third larval instar and pupal stages.

Discussion

Estimation of net adaptive values. It is important to reconsider the method of computation of net adaptive values from these life-cycle data for comparison with adaptive values obtained from relative frequency data of population cages. A close comparison between values determined by raising flies under crowded conditions and values obtained from relative frequency data would lend strong evidence towards finding the specific adaptive properties which these gene arrangements control in laboratory populations and which in turn may be effective in nature. In making this computation the following three properties have been used: fecundity of females raised in "500" vials, percentage survival in "500" vials (adults per 500 eggs), and the rate of development relationship (regression of days in preadult on survivors in the culture).

Because the most significant discrimination can be made between homokaryotypes on the basis of rate of development, the problem of expressing relative rates of development in terms of relative adaptive values will be dealt with first. It seems there may be two reasonable methods of approach: 1) to measure the potential of one female in terms of progeny realizable per day in the following generation, that is the measure of one "fly day," 2) to measure the potential of one female in terms of progeny realized by a definite period of time in the next generation. The former of these two methods was used by Spiess and Schuellein (1956): The reciprocals of total day values were taken as the relative rates of development. While WT/WT and KL/KL differed by six days in preadult stages when grown under near-optimal conditions, this method of calculating relative adaptive values resulted in underestimating relative value differences and was not a real-

istic measure for the population cage situation. It would be realistic if opportunity were allowed both slow and fast developing flies to emerge and join the breeding population without time limitation. Rate of establishment in the following generation would then be proportional to these reciprocals of total day values.

The objective is to discover what happens under population cage conditions. In the cage, food cups are changed at intervals; many developing individuals are discarded in that process, either because of slow development or because of late egg-laying. If the interval between changing food cups is short enough, slow developers will be selected against, and the relative numbers of survivors emerging by the time of change would measure relative fitness of the genotypes concerned. Therefore the second of the two above methods of approach would seem to be more realistic for the cage.

Under the conditions of "500" vials which may be considered comparable to population cage conditions, a hypothetical measure of survivors emerging in a limited time can be calculated, but the time limit must be chosen with some relation to the real situation before the numbers of survivors can be computed. This time limit was chosen by the following scheme: the interval during which a food cup remains in the cage is known to be 60 days. A sample of six representative food cups from different cages was isolated and records of emergence were kept until each food cup was exhausted of adult flies. The time required from introduction of the food cup into the cage until one half the total flies had emerged from that food cup averaged 55.2 days.

If a hypothetical "500" vial contains a mixture of the three karyotypes (as would be found in Cage 18R (Spiess, 1957) for example at point P when WT = KL = 0.5), then the average time it would take for emergence, that is when half of the flies have emerged, can easily be calculated by employing the data of Tables 1 and 3 and the regression values of Table 5 as follows:

If 500 eggs are deposited they will be in numbers:

Eggs:

WT/WT	WT/KL	KL/KL	Total
124	250	126	500

After differential viability the number of adults which would emerge will be if time is not limited:

Adults:

45.1	102.7	47.2	195

It would take the following times (in days) for preadult development at a density of 195 survivors:

Days:

WT/WT 31.92 WT/KL 32.93
KL/KL 35.81

This amounts to a weighted average of 33.39 days, or the time it would take for approximately half the flies in the vial to emerge. Using a simple proportionality with the fraction 55.2/60.0, the time of 36.29 days is obtained for the time interval during which the hypothetical "500" vial would remain in the population cage.

Table 6 illustrates the method of converting the rate data into relative adaptive values. The regression lines of figure 1 only give the average time it takes for cultures to come to eclosion. Some cultures come later, others earlier. By using the standard error of estimate of each regression line, the total expected number of emergence averages can be calculated by the area under the normal curve method. These total proportions observable by 36.29 days give relative measures of karyotype components of the 195 survivors. The net adaptive values (W) in table 6 then result. These W values correspond closely with values obtained in the population cage 18R (Spiess, 1957) for a single solution (WT/WT = .86, WT/KL = 1.00, KL/KL = .48).

TABLE 6. *A calculation of net adaptive values ($\bar{W}$) based on the area under the normal curve method*

Karyotype	Days	σ	$\frac{x}{\sigma}$	Area	Total area
WT/WT	36.29				
	−31.92				
	4.37	1.723	2.536	.4944	.9944
WT/KL	36.29				
	−32.93				
	3.36	1.291	2.603	.4953	.9953
KL/KL	36.29				
	−35.81				
	0.48	1.796	0.2673	.1053	.6053

	WT/WT	WT/KL	WL/KL
Therefore:			
Adults after selection:	44.85	102.21	28.57
Eggs before development:	124	250	126
Proportional change:	.3588	.4088	.2286
$\overline{W}$ (net adaptive value):	0.88	1.00	0.56

Now the question arises: what would happen to these adaptive values if food cup intervals were different from the interval chosen in the above analysis? Using the same method and the same regression constants, adaptive values have been calculated for increasing food cup intervals in table 7. It is quite evident that in order to hold adaptive values of these karyotypes constant the interval must be rigidly adhered to. The possibilty of shifting adaptive values by using different food cup intervals is currently being tested. The WT arrangement would be at such a great advantage with short food cup intervals as to completely eliminate the KL arrangement, while with a long interval the adaptive values are reversed with KL slightly at an advantage over WT.

As WT becomes more frequent, the average days for emergence of flies from a food cup will be less, for example when WT = 0.7, KL = 0.3, a hypothetical "500" vial would have 192.5 survivors but the average time of development would be 32.7 days compared with 33.4 days when WT = KL. If the interval of food cup removal remains constant the final adaptive values should remain constant nevertheless.

General considerations. It is interesting to reflect on the point that in the locality from which these flies came at elevation of 8,000 feet in Yosemite National Park, the WT arrangement occurs at high frequency (87%) while KL is

TABLE 7. *Relationship of relative adaptive values ($\bar{W}$) to rate of food cup change*

The limit within a generation corresponds to the total survival determined by relative viability and fertility of karyotypes.

Food cup interval in days	Relative W's		
	WT/WT	WT/KL	KL/KL
32	1.96	1.00	0.066
33	1.25	1.00	0.103
34	0.985	1.00	0.180
35	0.902	1.00	0.314
36	0.885	1.00	0.499
37	0.884	1.00	0.681
Limit within a generation	0.878	1.00	0.919

second in frequency (7%). Only in rate of development do homokaryotypes for these arrangements differ when grown under conditions which are variable in microenvironmental factors (as in "500" vials). In fecundity and viability they are not demonstrably different though the heterokaryotype is slightly higher than the homokaryotypes in these two respects. Can this difference in rate of development be sufficient to account for the constant difference in relative frequencies of these arrangements in nature?

At 8,000 feet in the Sierra Nevada of California, *D. persimilis* is not likely to have time for more than two generations in the season from June to September. The interval during which flies may reach a part of the life cycle resistant to winter cold might be very crucial. A slow developing fly would probably be at a disadvantage in such a situation. It is tempting to postulate that high frequency of the WT arrangement is largely due to its inclusion of genes which produce more rapid development. A definite answer to this problem might be found in a comparative study of developmental rates among populations from one end of the altitudinal transect to the other. The presence of KL arrangement produces a heterokaryotype which has slight superiority in viability and fecundity, and in spite of a slight lowering in rate of development is sufficiently superior to the other karyotypes to maintain the KL arrangement at a constant frequency in this locality.

Summary

(1) Karyotype combinations of the Whitney (WT) and Klamath (KL) arrangements of chromosome III from *Drosophila persimilis* native to an 8,000 ft. locality in Yosemite National Park were tested for the following adaptive properties: egg-laying capacity, survival of preadults, rate of development, and rate of female maturation. Individuals tested were grown on a volume of cream of wheat–molasses food about equal to that in a population cage food cup, in vials, and under varying densities from 50 to 500 eggs per vial. Strains were identical with those used in population cages described earlier. The temperature was 16° C.

(2) Egg-laying capacity of females raised under conditions of high larval density does not differ significantly from that of females raised under near optimal conditions, that is, homokaryotype WT and KL are nearly equal at about 19 eggs per day while the heterokaryotype is slightly superior at 21 eggs per day per female.

(3) High environmental variance is more likely produced by differences in microenvironmental factors between cultures other than larval density because there is no significant correlation between fecundity and number of survivors in a culture.

(4) Increasing density has no significant effect on percent survival of preadult stages within the limits tested (up to 500 eggs per vial), but the overall survival is about half that under near-optimal conditions. Apparently low average survival indicates high average contamination, but the variance between vials is very great indicating that microenvironmental conditions other than density are highly variable and that preadult stages of development are very sensitive to such conditions.

(5) In highest densities as well as under near-optimal conditions, the WT/KL karyotype has highest average survival by about the same magnitude of difference from the homokaryotypes which are nearly equal, though the within cross variance (between vials) is very large, and the sixteen-fold difference in variance between WT/KL vs. homokaryotypes and WT/WT vs. KL/KL is thereby concealed. The superiority of WT/KL in survival of preadult stages may be real for cultures in which microorganism contaminants can be held in check as in the sterile near-optimal cultures and in the high density cultures described where

there are sufficiently large numbers of larvae consuming microorganisms.

(6) In developmental rate of preadult stages, WT/WT surpasses KL/KL by approximately three days at all densities, while the heterokaryotype is intermediate. Under the wide variety of microenvironmental conditions possible in a population cage it is likely that these differences in developmental rate would be distinct and measurable.

(7) The three karyotypes do not differ significantly in rate of maturation (days from eclosion to oviposition).

(8) Net adaptive values based on relative survival within a defiinite time interval are calculated, and the close correspondence with the adaptive values obtained from population cage relative frequency data is discussed.

(9) It is postulated that high frequency of the WT arrangement in nature may be largely due to its advantage in more rapid development, when the time interval during which reproduction can take place is so critical for the species. The presence of the KL arrangement can be explained by its effect in the heterokaryotype which slightly surpasses homokaryotype WT in fecundity, viability, and greater uniformity in the relationship between developmental rate and density of culture.

Acknowledgments

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THE EVOLUTIONARY SIGNIFICANCE OF RARE MATINGS IN ANIMAL POPULATIONS

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INTRODUCTION

For evident reasons, field studies of the population ecology of rare or sparsely distributed animals are almost non-existent. Less easily explicable is the dearth of theoretical papers concerned with ecological factors which may come into play for sexually reproducing species at low density.

Andrewartha and Birch (1954:333, 337–43) state the lack of studies of "underpopulation," noting possible reduction of the innate capacity for increase because of the failure to find mates. They give a detailed discussion of mate-finding in the sheep tick, *Ixodes ricinus*, based on work by Milne. They also discuss briefly (op. cit.: 695–697) possible effects, at population low, on genetic composition in a fluctuating population. Since their work, Philip (1957) has presented a study of population growth (or extinction) based on analysis using the probability of fertilization of females in a random model in combination with the logistic curve.

Numerous papers presented by Wright (e.g., 1931, 1940, 1948) have noted the relative importance of random fluctuations in gene frequency (as opposed to changes in frequency due to natural selection) in populations with small effective population size. Summaries of the evolutionary significance of Wright's work can be found in Dobzhansky (1951) and in Li (1955). Pertinent to this study are Wright's conclusions as to the importance of populations of small effective size in evolution. Thus Wright (1931:157) states: "In too small a population (1/4N much greater than u and s) there is nearly complete fixation, little variation, little effect of selection and thus a static condition, modified occasionally by chance fixation of new mutations, leading inevitably to degeneration and extinction." [2]

He later adds (1948: 280): "I suspect that 'inevitably' is too strong a word as used above, but otherwise this quotation still represents my position on the importance of population structure in evolution."

Since sparse populations are apt to have a small effective population size, they fulfill the conditions under which random fluctuations or gene drift may significantly alter gene frequencies.

It is my purpose in the present paper *first* to present a model for studying random mate-finding with a tentative attempt at application to a natural case, and *second* to discuss low density effects which in particular cases considered could themselves cause high selection coefficients resulting in strong natural selection in populations with small effective size.

ENCOUNTERS IN RANDOMLY MOVING PARTICLES AT CONSTANT SPEED

Given a set of particles moving at random at a constant velocity (v) on a plane surface. Let a particle sweep a path of width 2r (one r to each side of the particle). The area swept by a particle in unit time would then be

$$A = 2rv$$

If the area is "populated" with other particles than the first, then the number

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[2] In the above, N is "population number"; u, mutation rate; and s, the selection coefficient.

of particles swept by the first during unit time would be

$$\theta = 2rvn$$

Here n is the density per unit space of the other particles. However, if all particles are in motion then the velocity under consideration for the sweeping particle is its velocity relative to the velocities of the other moving particles. The mean relative velocity in two dimensions can be shown to be (cf. Appendix)

$$\bar{v}_r = 1.2732v$$

Thus the average number of particles swept on a plane surface by a single particle per unit time would be expected to be

$$\theta = 2(1.2732)rvn$$

If it is assumed that one half the particles are "male" and one half "female" then the number of females swept (or encountered) by a moving male and vice versa would be expected to be

$$\theta = 1.2732rvn$$

For three dimensions analogous reasoning gives

$$\theta = 2.0944r^2vn$$

The important parameters are "r" which is a measure of detecting ability (which of course may vary seasonally as well as with habitat); "v" or velocity of movement an indicator of locomotor ability and activity; and "n" or adult density.

The number of encounters of a single male with females, or vice versa, over time "t" would be

$$\theta t$$

Since the encounter of two individuals gives a single collision, the total collisions expected between males and females (males ½ of population) would be expected to be the number in the population "N" times the collision rate "θ" times the duration "t" all divided by two

$$\frac{N\theta t}{2}$$

Philip (1957) used the following model in combination with the logistic curve to study effects of sparsity on population growth. I am repeating part of his presentation here although modified somewhat. Let n/2 be the density of adult males capable of fertilizing females. Let $\bar{v}_r$ be the mean relative velocity of females relative to male velocities. Let 2r be the detecting range of the male (one r to each side of the particle). Let $L = (\bar{v}_r t)$ be the total distance traveled by a female during reproduction time t. The probability of a female missing males when traveling interval ΔL is

$$1 - 2r\frac{n}{2}\Delta L$$

Since there are $L/\Delta L$ such intervals the probability of not "hitting" a male and thus not being fertilized is

$$(1 - rn\,\Delta L)^{L/\Delta L}$$

The limit of this expression as ΔL approaches zero is

$$e^{-rn\bar{v}_r t} \quad \text{or} \quad e^{-\theta t}$$

The probability of at least one hit and thus the probability of fertilization, assuming males are never exhausted nor bored, is

$$1 - e^{-\theta t}$$

This is simply one minus the zero-frequency class of a Poisson distribution with mean equal to θt, i.e., the number of collisions expected for a single particle.

Random Encounters in the Box Turtle, *Terrapene carolina*

In view of the many unknown variables at play in natural populations, it may seem rash to attempt to apply the models discussed to a natural case. However, attempted applications of theoretical population dynamics to natural instances are particularly needed. Further, it is often in the very enumeration of biological departures from a theoretical model that the use of the model itself is productive. I am aware that the following

application is based on considerable guesswork, yet the results seem useful if carefully interpreted.

Stickel (1950) studied home range and populations in the box turtle (*Terrapene carolina*) at the Patuxent Research Refuge in Maryland. The area and methods of study are well described in her monograph. Stickel's data are unique in that continuous tracings of animal movement (made possible by attaching spools of thread to the animals concerned) were obtained. Thus it is possible from her data to obtain a mean velocity of movement affected by all stops and periods of inactivity of the animal. This is a mean velocity of activity, measuring not only how fast, but also how often, the animal moved.

Dr. Stickel has kindly sent me her original maps of *Terrapene* movement. Movement of five turtles has been measured (192 ♀, 424 ♂, 476 ♀, 492 ♀, 629 ♂) as exemplified at various intervals from July 6 to July 17, 1945. (One of these individuals (629 ♂) was observed mating during this interval.) I have taken the total hours elapsed (885) together with the corresponding feet moved (7375) and obtained a rate in feet/hour of 8.3. This figure includes all periods of inactivity. Table 1 gives the individual figures for each of the five turtles.

TABLE 1. *Movement of* Terrapene carolina *based on measurements of Stickel's maps (1950 and unpubl. maps)*

Turtle	Period	Hours elapsed	Feet travelled	Feet/hour
476 ♀	July 6–17	229	1575	6.88
629 ♂	July 6–14	196	894	4.56
492 ♀	July 6–10	98	787	8.03
424 ♂	July 6–11	109	1607	14.74
192 ♀	July 11–17	253	2512	9.93
Total	July 6–17	885	7375	8.33

Allowing one month (720 hours) reproductive period during a year as a conservative estimate, a detecting range of male-female of ten feet and an activity

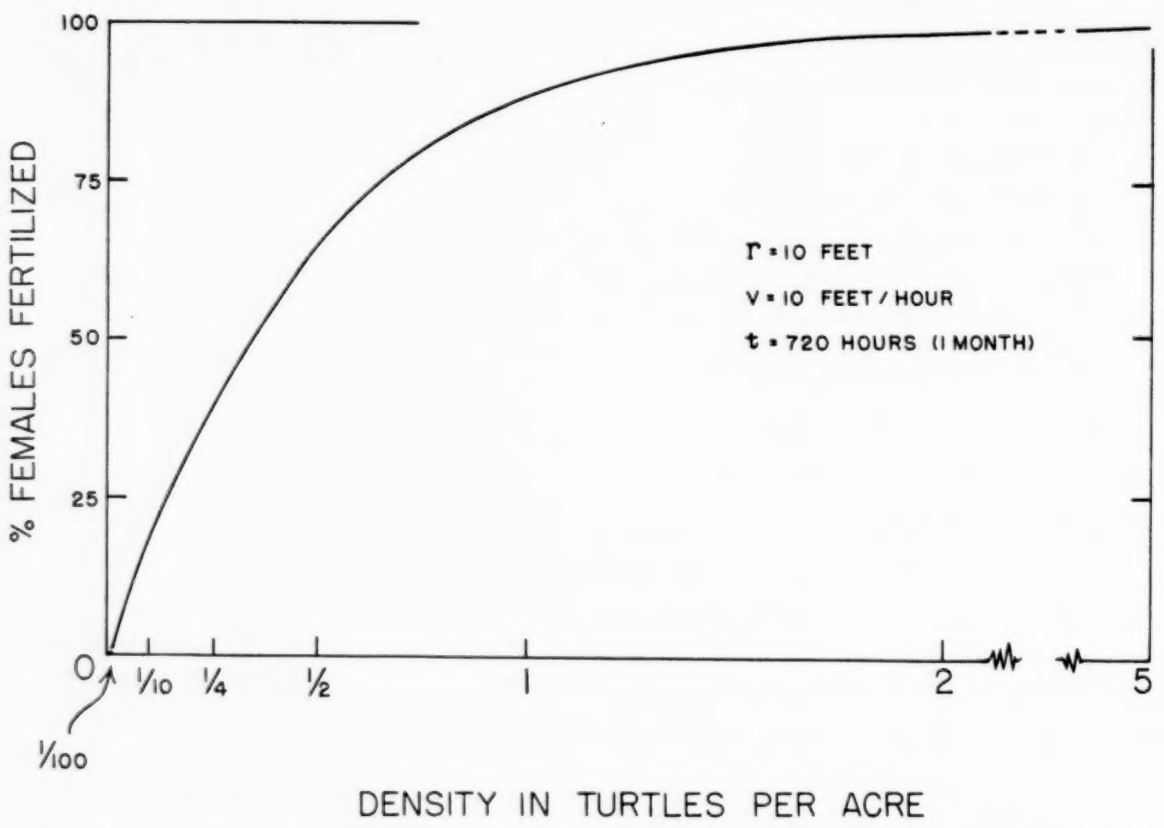


FIG. 1. Relation between per cent females fertilized and density in adults per acre for the box turtle *Terrapene carolina*. A sex ratio of one is assumed. Detecting range is taken as ten feet, activity rate as ten feet per hour, and reproductive season as one month.

TABLE 2 (PT. 1). *Number of encounters of a female with males*
(720 hours a year for 1 year)

	V = 5 feet/hour				V = 10 feet/hour				V = 20 feet/hour			
	Detecting range				Detecting range				Detecting range			
Density	100 ft.	10 ft.	2 ft.	1 ft.	100 ft.	10 ft.	2 ft.	1 ft.	100 ft.	10 ft.	2 ft.	1 ft.
5/acre[1]	52.61	5.26	1.05	0.53	105.2	10.52	2.10	1.05	210.4	21.04	4.21	2.10
1/acre	10.52	1.05	0.21	0.10	21.04	2.10	0.42	0.21	42.09	4.21	0.84	0.42
1/2 acres	5.26	0.53	0.10	0.05	10.52	1.05	0.21	0.10	21.04	2.10	0.42	0.21
1/4 acres	2.63	0.26	0.05	0.03	5.26	0.53	0.10	0.05	10.52	1.05	0.21	0.10
1/10 acres	1.05	0.10	0.02	0.01	2.10	0.21	0.04	0.02	4.21	0.42	0.08	0.04
1/100 acres	0.10	0.01	0.002	0.001	0.21	0.02	0.004	0.002	0.42	0.04	0.008	0.004

[1] One acre equals 43,560 square feet.

TABLE 2 (PT. 2). *Number of encounters of a female with males*
(720 hours a year for 10 years)

	V = 5 feet/hour				V = 10 feet/hour				V = 20 feet/hour			
	Detecting range				Detecting range				Detecting range			
Density	100 ft.	10 ft.	2 ft.	1 ft.	100 ft.	10 ft.	2 ft.	1 ft.	100 ft.	10 ft.	2 ft.	1 ft.
5/acre	526.1	52.61	10.52	5.26	1052.2	105.2	21.04	10.52	2104.5	210.4	42.09	21.04
1/acre	105.2	10.52	2.10	1.05	210.4	21.04	4.21	2.10	420.9	42.09	8.42	4.21
1/2 acres	52.61	5.26	1.05	0.53	105.2	10.52	2.10	1.05	210.4	21.04	4.21	2.10
1/4 acres	26.30	2.63	0.53	0.26	52.61	5.26	1.05	0.53	105.2	10.52	2.10	1.05
1/10 acres	10.52	1.05	0.21	0.10	21.04	2.10	0.42	0.21	42.09	4.21	0.84	0.42
1/100 acres	1.05	0.10	0.02	0.01	2.10	0.21	0.04	0.02	4.21	0.42	0.08	0.04

TABLE 2 (PT. 3). *Number of encounters of a female with males*
(720 hours a year for 20 years)

	V = 5 feet/hour				V = 10 feet/hour				V = 20 feet/hour			
	Detecting range				Detecting range				Detecting range			
Density	100 ft.	10 ft.	2 ft.	1 ft.	100 ft.	10 ft.	2 ft.	1 ft.	100 ft.	10 ft.	2 ft.	1 ft.
5/acre	1052.2	105.2	21.04	10.52	2104.5	210.4	42.09	21.04	4208.9	420.9	84.18	42.09
1/acre	210.4	21.04	4.21	2.10	420.9	42.09	8.42	4.21	841.8	84.18	16.83	8.42
1/2 acres	105.2	10.52	2.10	1.05	210.4	21.04	4.21	2.10	420.9	42.09	8.42	4.21
1/4 acres	52.61	5.26	1.05	0.53	105.2	10.52	2.10	1.05	210.4	21.04	4.21	2.10
1/10 acres	21.04	2.10	0.42	0.21	42.09	4.21	0.84	0.42	84.18	8.42	1.68	0.84
1/100 acres	2.10	0.21	0.04	0.02	4.21	0.42	0.08	0.04	8.42	0.84	0.16	0.08

rate of ten feet per hour it is possible to estimate the number of random passes (within ten feet) using the model discussed. Although I think the above values are fairly realistic, a range of values about each parameter is presented. Using a range of values it should be possible to straddle the range of natural values for combinations of detecting, activity, and reproductive period found in nature (table 2).

The density of the population studied by Stickel was about five adults per acre. At this density and $r = 10$, $v = 10$, a female would be expected to pass within ten feet of a male ten times during a one month period by chance alone.[3] Under such conditions, 100% of the female

[3] The calculation is

$$\theta t = \frac{5 \times 10 \times 10 \times 1.2732 \times 720}{43{,}560} = 10.5223.$$

TABLE 3. *Probability of fertilization of female during time t.* This is equal to $1 - e^{-\theta t}$.

$e^{-\theta t}$	θt	$1 - e^{-\theta t}$
1.0000	0.00	.00
.9900	0.01	.01
.9512	0.05	.05
.9048	0.10	.10
.8521	0.16	.15
.8025	0.22	.20
.7483	0.29	.25
.6977	0.36	.30
.6703	0.40	.33
.5016	0.69	.50
.3679	1.00	.63
.2491	1.39	.75
.1353	2.00	.87
.0498	3.00	.95
.0183	4.00	.98
.0067	5.00	.99

population would in all probability be fertilized each year (cf. table 3 and fig. 1), even if lacking biological adaptations to facilitate mate-finding. At a density of one per acre a female would be expected to pass within ten feet of a male twice in one month (720 hours). Under such conditions 87% of the female population would be expected to be fertilized. At one per two acres the per cent expected would be 63%. At one per four acres, 41%, and at one per ten acres, 20%.

Unfortunately the interpretation of the above figures in terms of population survival and balance is hampered by a lack of knowledge of reproductive rates and mortality rates. There is no life-table available for *T. carolina,* nor in fact for any turtle. However, the box turtle usually lays four or five eggs at a laying (Carr, 1952). This presumably takes place once a season. A special attribute is the ability of females to store viable sperm (Ewing, 1943; Finneran, 1948). One female (Ewing, op. cit.) produced five fertile eggs four years after contact with a male. Nichols (1939) suggests that sexual maturity in males is reached in 12–14 years. He further suggests that the life expectancy of a box turtle is between 40 and 50 years. Oliver (1955: 284) notes that two females 35 and 56 years old laid fertile eggs. With such long-lived animals with females capable of sperm storage, fertilization need not occur for each female every year. I think that box turtles could easily maintain a stable population at a density of one per two acres, and perhaps maintain a stable population at a density as low as one per ten acres without any specialized mate-finding traits other than sperm storage. At one per ten acres over a period of twenty years, a female would be expected to pass within ten feet of a male four times. With the advantageous effects of sperm storage, this might be sufficient to maintain a stable population. Taking this into account I think that box turtles could at least maintain a stable population, as regards problems of mate-finding, at a density as low as one per four acres without other special mate-finding traits.

ASSUMPTIONS IN THE BOX TURTLE MODEL APPLICATION

There are a number of assumptions involved in the preceding application. The major ones are:

1) Constant density over the reproductive period.
2) For all turtles the same (constant) velocity of movement in straight line segments of considerable length between turns.
3) Random movement of turtles.
4) Constant detecting range over the reproductive period, and infallible detecting.
5) Homogeneity of habitat or surface.
6) Fertilization always resulting after detection.
7) Sex ratio of one.
8) A population distributed at density n, but very large, sufficiently so that the equation for θ can be regarded as deterministic.

The above assumptions are necessary if one wishes to specify the number of female box turtles fertilized. If one

simply wishes to specify the number of males passed within a given number of feet by a female then (4) and (6) are not necessary.

Perhaps a serious objection is the constant straight-line motion (here the model is analogous to the constant speed gas model of Clausius (cf. Kennard, 1938: 105)). Specifying a frequency distribution for the velocities of individuals would certainly be preferable, yet in terms of the mean collision rate this would probably change the estimates used very little. (When molecules are considered as having a maxwellian distribution of velocities there is little change in mean collision rate as estimated from the constant-speed Clausius model (cf. Kennard, op. cit.: 113).) For the mean collision rate alone there is little reason to postulate a frequency distribution for the velocities.

There is a more serious logical objection to the use of the model. As employed here the equation for θ is essentially deterministic, the mean collision rate predicted applying in an infinitely large population of a given density. The model in the above sense is most applicable to the case of a wide-ranging species abundant in total numbers but distributed at a given density throughout its range. It is not directly applicable to the case of a numerically small population without the additional consideration of variance in the mean collision rate. Thus there are two distinct questions involved in the use of the model. First, what is the probability that a male will encounter a female? and second, what is the probability that a group will reproduce itself? Whereas the answer to the first question does not depend on group size, the answer to the second depends both on the answer to the first and on group size. Thus a large population of turtles at density n might reproduce itself whereas a small population sometimes might and sometimes might not. If the mean collision rate were high, but nevertheless it were sufficiently probable during a number of consecutive seasons for no or very few females to be fertilized, then the species would not persist. For usefulness in application to numerically small populations the variance of the mean collision rate is important. Given a mean collision rate, the probability distribution of hits (or male-female encounters) can be specified as Poisson. However, variance in the mean collision rate itself is crucial. In general, within the range of the application attempted, I think the assumptions not so extreme as to invalidate the conclusions reached.

Low-Density Considerations in Natural Populations

The foregoing model considers the probability of matings at random, this probability being a function of four parameters: density (n), locomotor activity (v), detecting range (r), and reproductive period (t). Without recourse to a particular mathematical formulation, I would like here to consider various aspects of the mate-finding problem in terms of these parameters.

In this discussion the following operational definitions will be used. The *geographic range* (G) of a species is the total area (or volume where three dimensions are concerned) circumscribing the occurrence of individuals of that species. In this context it is simply a spatial definition. The distribution of the species within the geographic range need not be nearly continuous. The *ecological range* of a species is the total area of environment occupied by the species within the *geographic range*. Thus when the *geographic range* circumscribes an area of homogeneous habitat, the *ecological range* and the *geographic range* are co-extensive. *Homogeneity* of an area implies that there are no influences external to an individual, other than those stemming from others of its own species, which cause it to select one subarea in preference to another. *Detecting range* (r) may be thought of as the maximum limit

of detectability for a member of one sex to perceive the existence of an individual of the opposite sex. This of course may vary seasonally, sexually, with habitat, etc.

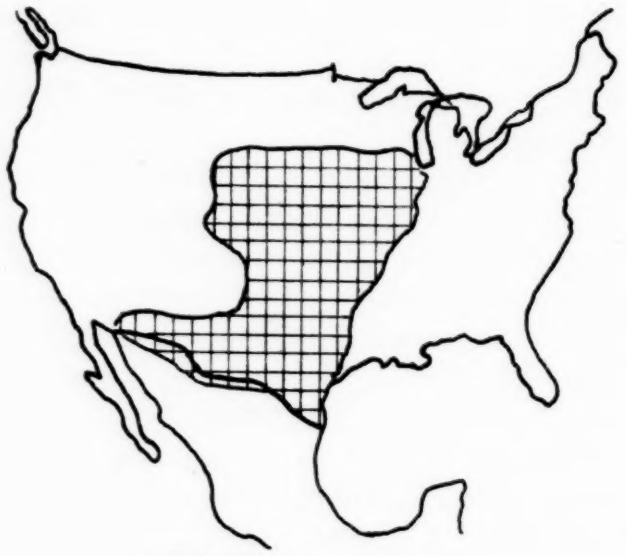
Description of three typical vertebrates showing different G/r ratios may be given (fig. 2):

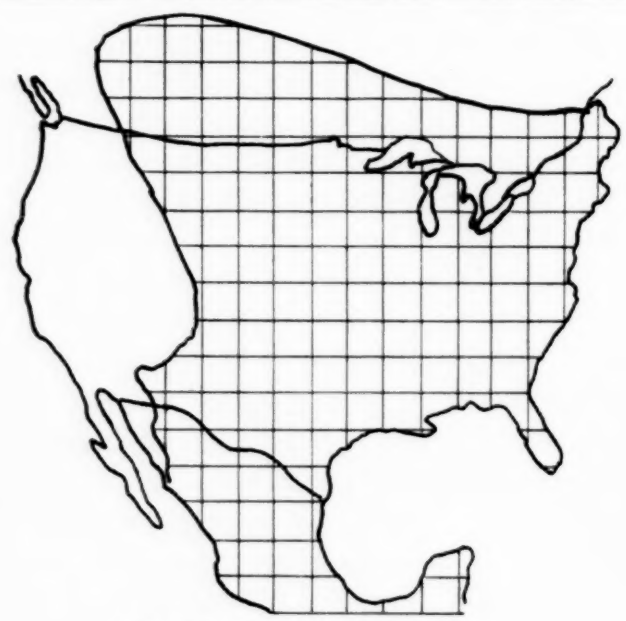
(a) *Plethodon cinereus*: red backed salamander, less than 8 inches in length, living in humus, decaying logs on the floor of a (usually) hardwood forest. Geographic range is eastern North America. Detecting ability very slight, probably not greater than a foot.

(b) *Terrapene ornata*: ornate box turtle, less than 16 inches in length (in weight much greater than *P. cinereus*), lives in sandy, semi-arid areas, prairies, savannas, rarely woodlands. Geographic range is central United States. Detecting ability considerably greater than in *P. cinereus*, perhaps ten feet, perhaps considerably more.

(c) *Odocoileus virginianus*, whitetail deer, less than 10 feet in length (in weight much greater than *T. ornata*), lives in woodlands. Geographic range North America, primarily eastern. Detecting range much greater than for *T. ornata*, at least 1,000 feet, probably greater.

Viewed in a static way, it is obvious that natural populations present variations in the ratio of r areas to the total area G. However, this view is necessarily incomplete as locomotor abilities of animals must be taken into account. Locomotor abilities not only greatly affect the probability of detection, but also locomotor ability must be sufficient to effect juxtaposition of sperm and ovum after detection. If a sexually reproducing animal population is to establish itself in a new area, or maintain itself in an old





Geographic Ranges and Relative 'r's for Three Vertebrate Species

FIG. 2. Relative detecting range and geographic ranges for three North American vertebrates: Red-backed Salamander, *Plethodon cinereus;* Ornate Box Turtle, *Terrapene ornata;* Whitetail Deer, *Odocoileus virginianus.* The values depicted are relative only.

area, then the probability of sperm encountering ovum, usually one sex encountering the other but not necessarily (ex.: female encountering spermatophores in the salamander, *Ambystoma maculatum*), must be sufficiently high. For exclusively sexually reproducing species, mate-finding may become limiting. This case is apt to be realized in any animals of sparse populations, whether migrating into a new area, or simply persisting in an occupied area at a time of population low.

Numerical, Spatial, and Temporal Adaptations

Favorable changes in the parameters listed by me which increase the probability of fertilization result from: 1) the increase in r, 2) the decrease in G (for given N), 3) the increase in size of N (adult population) for a given G, 4) the increase of locomotor activity (v), 5) the increase of t.

All these listed factors may interact favorably from the point of view of the survival of a given population.

Remembering that density (n) equals N/G, then consider for the moment the cases where the parameters (v, r, G and N) are the main variables. Assume that other factors (specific biological adaptations) are largely inoperative. Also assume that sparsity is a significant factor.

A sufficiently high adult density might be maintained in the following ways: 1) Shrink G (for a given N) either by actually shrinking G itself or effectively by a preference for subareas within G (e.g., ecological restriction to definite areas within G). 2) Shrink G (for a given N) at reproductive season only. 3) Increase r by increasing sense perception or perceptibility (sight, scent, sound). 4) Increase r at reproductive season only (2 and 4 may occur simultaneously). 5) Shrink G/r by herding or schooling tendencies. 6) Increase N (for a given G) to the point where sparsity is no longer a problem. 7) Increase locomotor activity. Some of these possibilities are illustrated in figure 3.

Herding effectively lowers G/r and at the same time leaves available to the population the total resources of the former G for food, shelter, etc. Thus in herding, a population can utilize a large area although maintaining a low G/r ratio. Also a seasonal breeder can use the total resources of a large G during most of the year. Yet at the critical breeding time G/r can be made lower by either increased r, lowered G (breeding habitat) or both simultaneously. These two solutions would involve selection for innate behavioral characteristics.

Selection for a habitat of *limited area* within the G can favorably adjust the G/r ratio, but this does not permit the population to utilize the total resources of G, the geographical range.

There are numerous examples of increase in r, particularly by means of odors and sounds (cf., for example, Alexander (1957), who has summarized sound production and associated behavior in insects).

With regard to t, this might be lengthened by increasing the length of the reproductive period, or by increasing length of adult life. A breeding season unaccompanied by any special adaptations would be disadvantageous in a sparse random mating population since all chance meetings of males and females at other times would be wasted. With concomitant adaptations, however, a reproductive season can be advantageous since concentrations of adults in breeding condition can be effective for short or very short periods of time. Thus the density of adults may be momentarily very great in an area incapable of supporting the total biomass of these adults for sustained periods.

The following examples are considered in a descriptive sense, not in the sense of explaining the evolutionary origin of the adaptations concerned. There remains, of course, the possibility that selection during past times of low density contributed to the presence of traits in these populations today even though at present the

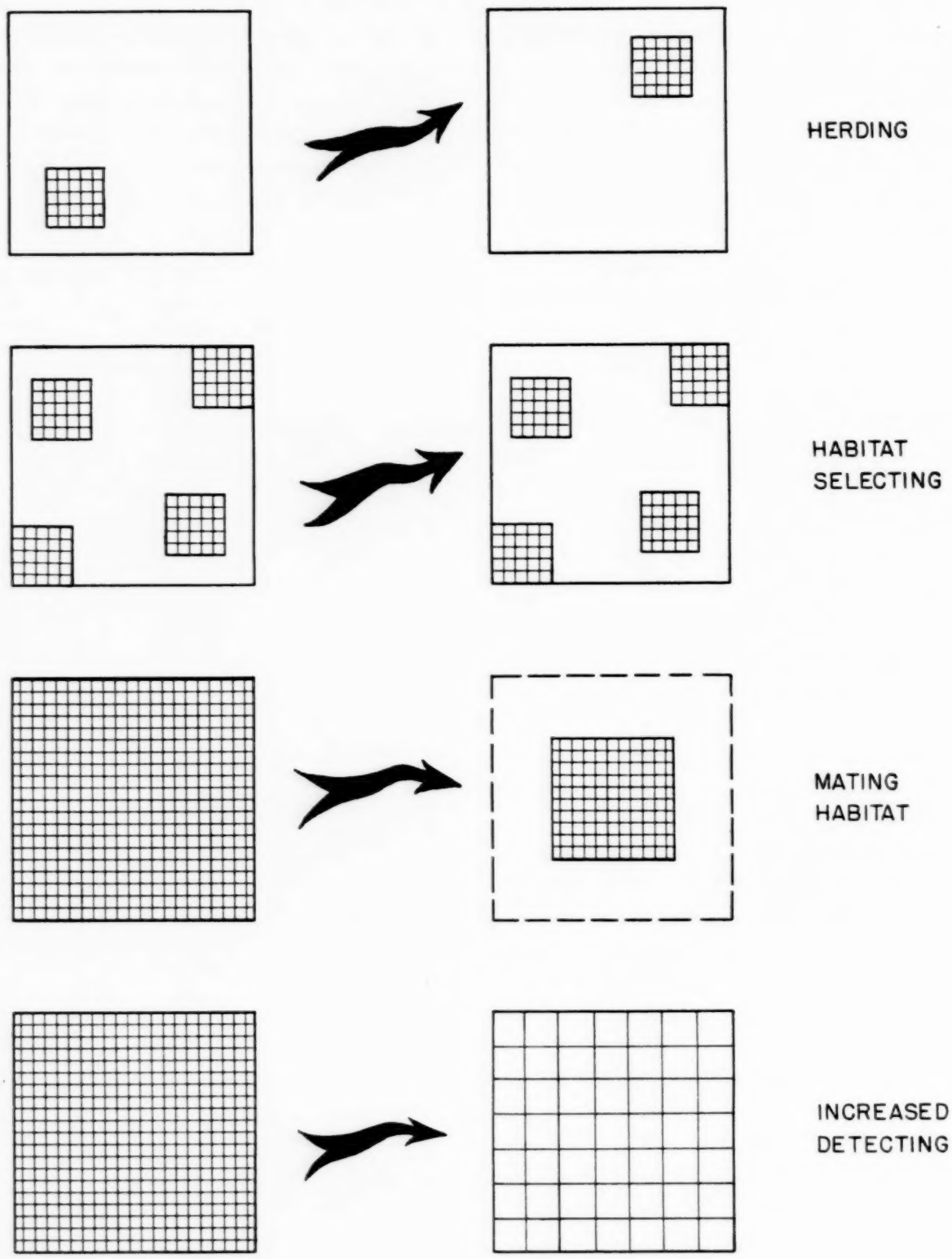


FIG. 3. Possible changes in geographic range (G) relative to detecting range (r) without changing population size.

populations may be by no means sparse.

The tree frog, *Hyla versicolor,* of eastern North America is a species which concentrates in woodland pools for breeding; thus its G is effectively changed. Further, the males are vociferous at breeding time, thus r is also changed. On the other hand, the southern bullfrog, *Rana grylio,* does not change its G greatly, but does change r, calling vocif-

erously during the breeding season from the ponds and swamps it occupies throughout the year. Jefferson's salamander, *Ambystoma jeffersonianum*, probably does not change its r, but it does change its G, concentrating in woodland pools for breeding.

Specific Biological Adaptations

There are many specific biological adaptations for solving the problem of mate-finding. Logically these may be divided into two classes: adaptations which affect mate-finding as such, and adaptations which increase the effectiveness of a single mating. The distinction in practice is not always clear. The most favorable adaptation affecting mate-finding is probably memory. The use of memory accompanied by a home range for one of the partners to a mating can almost eliminate the problem. For example, if at a time of high population density a male had found females at certain dens or within certain home ranges, then at a time of low density his search may be limited to the dens or home ranges which he remembers. His search is by no means random.

A group of characteristics which may facilitate mate-finding involves non-homogeneity of habitat coupled with particular orientations and habits shared by males and females of the same species. For example, both sexes of common box turtles may congregate beneath a strawberry bush, the original orientation being not to members of the opposite sex but to the bush.

Selection for such seemingly non-adaptive characteristics at low population could produce results indistinguishable from those expected by gene drift. Later non-sparse populations could have a non-adaptive character following a period of population low. In certain cases it might be impossible to determine whether drift or selection were the causative factor.

Favorable adaptations increasing the effectiveness of a single mating are numerous. A few are: 1) Production of large numbers of young. 2) Longer adult life of the offspring (affecting t). 3) Lifetime mating of a male with a female. 4) Storage and repeated use of sperm from a single mating by the female.

Evolutionary Significance of Sparsity

Some of the above adaptations may almost eliminate the randomness in mate-finding. Mate-finding is a problem which must be solved by any sexually reproducing population, and it is not surprising to find that most existing species show adaptations for this, whether through increasing r by means of sound, scent or sight, whether by herding, by seasonal concentrations, or by using memory or mating for life. One can only say that the complete failures in this regard are awarded immediate extinction. Partial failures may find themselves at a strong disadvantage, and Philip (1957) has shown in a sufficiently general way the competitive advantage in population growth enjoyed by a "social" species over a similar one in which mate-finding is at random.

Herding or Schooling

Populations which are by no means sparse today may show low-density adaptive traits inherited from their past. Granting this, it is tempting to speculate upon the relative rapidity with which a behavioral trait such as herding or schooling might be selected. Given a polymorphic population, the genotypes without a herding tendency could all fail to find mates and be eliminated at a single time of critical density whereas genotypes with a herding tendency could survive. The probability of the future survival of a population subjected to the drastic reduction in genetic variability which might result might be low. However, it seems that in the evolutionary time scale such events might be of common enough occurrence that successful

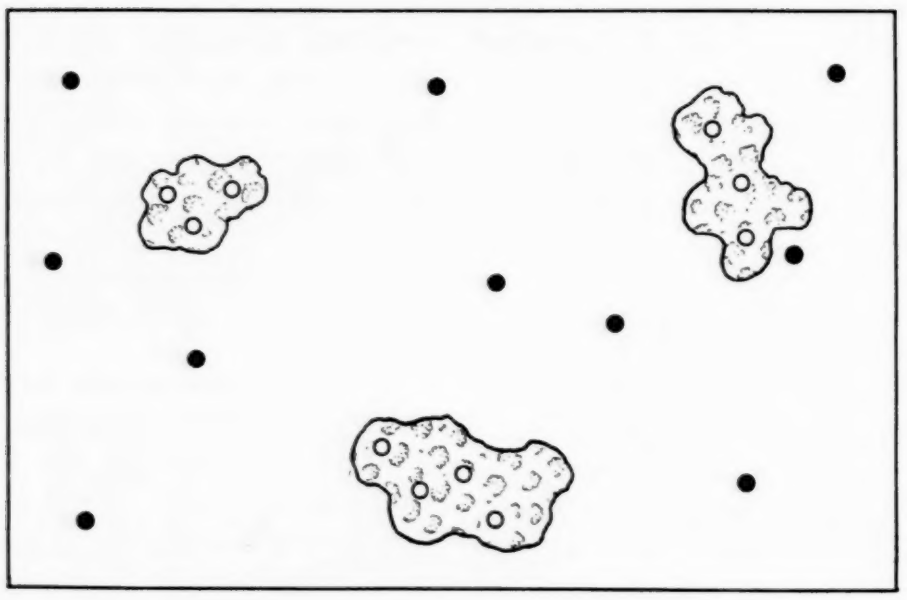


FIG. 4. Reversal of selection due to density factors in two areas, one of continuous grassland with isolated tracts of woodland and one of continuous woodland with isolated tracts of grassland. Compare with figure 5. Only in the small areas is the density high enough to permit population survival.

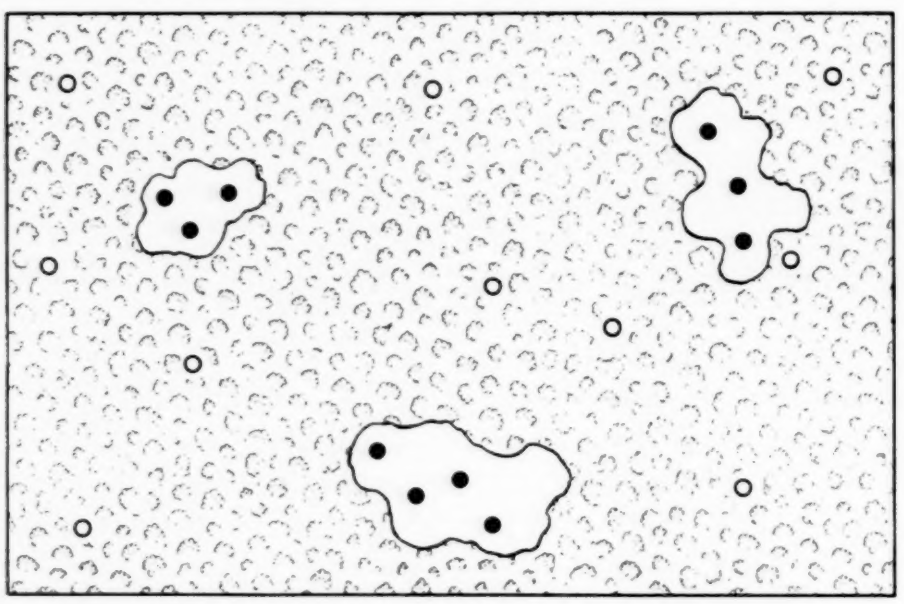


FIG. 5. Reversal of selection due to density factors in two areas, one of continuous grassland with isolated tracts of woodland and one of continuous woodland with isolated tracts of grassland. Compare with figure 4. Only in the small areas is the density high enough to permit population survival.

adaptation might be expected with something approaching a fairly high frequency. Of course there may be many advantages to herding, mutual protection as well as others (cf. Allee, 1938), which are not concerned with mate-finding, but the origin of herding in various taxa could be due to density factors having accelerated selection for traits connected with herding in any way.

Habitat Selection

The effect of maintaining a favorable G/r ratio could produce some interesting evolutionary-ecological interactions. For example, in an area of two habitats,

where one is of much less spatial extent than the other, there could be an accelerated natural selection for a character of specific adaptation for the smaller habitat, by virtue of the necessity of the sparse species to maintain itself above a critical density. This would be accelerated selection (by means of a density factor) for a physically adaptive genotype. It is thus conceivable that selection might operate in reverse in two areas for the same species: for example if there were one area with large extents of grassland dotted with small isolated tracts of woodland, and another with large extents of woodland and small isolated tracts of grassland (fig. 4, 5). In the first area selection due to a critical density factor would favor the survival of humid-tolerant genotypes. In the second, selection due to a critical density factor would favor the survival of arid-tolerant genotypes. Only in the small areas would G/r be below the critical point naturally leading to extinction. Once selected for, the population would be more or less restricted to the habitats of small area (assuming the selection is not for heterozygotes).

The above situation might be realized assuming the following conditions: a) mate-finding becomes critical; b) there is a polymorphic population with variously "preadapted" genotypes; and c) there is some method of orientation, direct or not, which results in a tendency to localization of the animals concerned in the habitat to which they are "preadapted."

Given three or four habitats, an original population which is polymorphic, and one continuous habitat matrix among which the others are dispersed, it is possible that there would be acceleration of selection of the original polymorphic species into the small and different habitats. Thus, within the same general conditions of climate, selection might act to limit the sparsely distributed animals to edaphically controlled areas of small extent, or areas in a stage of succession which are passed through relatively rapidly with the result that at any one time the habitat is represented only in small areas. Given a widely distributed polymorphic population oscillating considerably in abundance it is possible to have selection of the various genotypes for small habitat areas at a time of low density. Or imagine a polymorphic population colonizing a new area, in which numerous small diverse habitats are present (fig. 6). It is possible, if low density

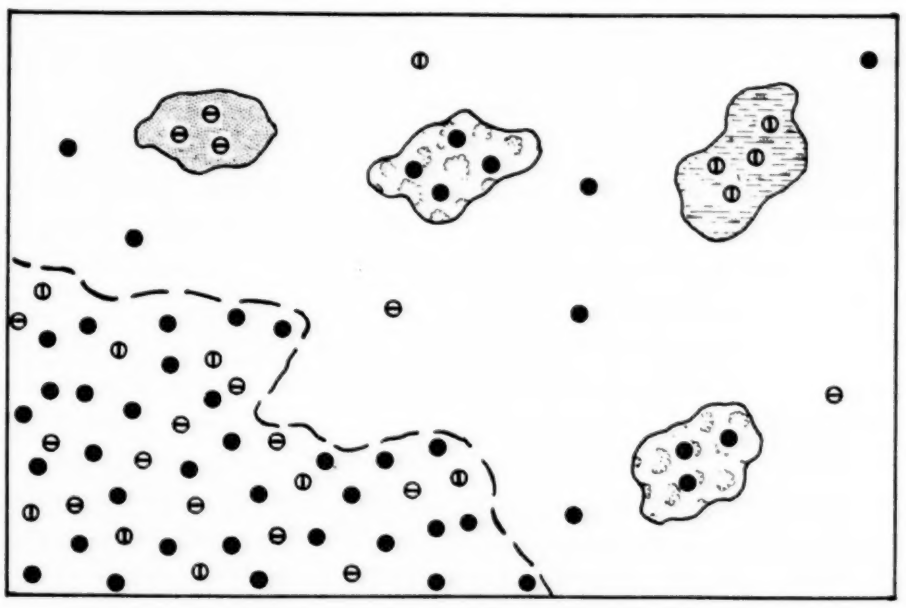


FIG. 6. Diversification of a polymorphic population into habitats of small area. In the small areas the density is high enough to permit population survival.

is critical and other assumptions stated above hold, that there will be a break-up and divergence of the population fringes into the small habitat areas. Again, once selected, the small isolated populations would be more or less restricted to the individual habitats, provided the selection were not for heterozygotes. Of course, if the favored genes were recessive then the character would be fixed in the population. It can thus be seen that there can be promotion of very high selection coefficients for factors involving orientation to habitats of small area at time of low density. This could result in the production of diversified rare populations.

A possible region in which one might expect such phenomena is in tropical areas of considerable relief and consequent extreme habitat divergence even in very localized areas. In broad terms, the cenozoic history of the central american tropics has been one of continued "colonizing" waves of animals (cf. for example, Simpson, 1943, 1953). Much of the variety in the species present there today is due to doubtless evolutionally old immigrant groups (e.g., the turtle *Dermatemys mawi* in southeastern Mexico), yet many of the forms are doubtless evolved in situ (e.g., species of the salamander family Plethodontidae and many of the frogs of the Hylidae and Leptodactylidae in southern Mexico). In the State of Veracruz, for example, Smith and Taylor (1948) list 14 species of the genus *Hyla* alone. Although it is easy to explain the diversity and rarity of many of the species because of the extreme diversity and localizations of biotopes, low-density factors may have speeded up and contributed directly in the rate of evolution into these areas. Of further speculative interest is the relative permanence of these species. Perhaps many of them are extremely temporary evolutionally speaking and will suffer extinction for reasons of gene fixation and consequent lack of genetic adaptability as predicted by Wright. Others may form a basis for continuing evolution. Similar reasoning may apply to the evolution of some of the diverse species of Brazilian *Drosophila* discussed by Dobzhansky and Pavan (1950: 13).

Accelerated Selection

In general as populations of sexually reproducing animals become sparsely distributed it is possible to have accelerated natural selection for characters previously having only slight adaptive value in themselves. In other words for factors concerned in any way with mate-finding it is possible to find a negative correlation between selection coefficients and density. I would say that natural selection could be expected to be important relatively frequently in sparse populations of small effective size. There is no contradiction between this statement and that by Wright quoted before. His is of a more general nature and validity, and his statement of "little effect of selection" is meant to apply only to small or moderate selection coefficients. According to Wright "too small a population" is where 1/4N (N being "population number") is much greater than u (mutation rate) and s (selection coefficient). The high values for s which might be expected commonly at sparsity under conditions postulated here would render the cases discussed out of the scope of Wright's statement. Yet populations resulting from the selection postulated here could easily be within that scope.

My postulate is that in introducing ecological considerations of mate-finding and non-homogeneity of habitat, one might often expect high selection coefficients to operate in sparse populations. The relation of such selection to speciation and further evolutionary opportunity is problematical. Many populations resulting from such selection might be subject to almost inevitable extinction, but others might find new areas of adaptive opportunity, particularly in the case of herding animals which could still utilize all the resources previously available to them. In

the case of habitat selection there might or might not be migration between the isolated areas. If such existed, then there would be a situation of partially isolated local populations regarded by Wright (1940) as conducive to rapid evolution. If no migration or gene exchange were possible between the isolated populations then a great deal would depend on chance and on the carrying capacity and permanence of the small area to which the animals have been forced. Many such populations might remain low in number and become extinct from lack of adaptability due to already reduced genetic variability as well as to possible further effects of random gene fixation. Others might build a population large enough for drift to be ineffective even though the inhabited area were small. In other cases the habitat itself might enlarge considerably in extent and the species flourish, particularly where succession was rapid. In all these cases the most important factor is the long-term value of the adaptations strongly selected for at low density as opposed to the detrimental effects of loss of genetic variability and consequent loss of "adaptability." Even if the probability of survival of a single population upon which drastic habitat selection (and consequent reduction of genetic variability) has taken place is low, the question remains of how often the occurrence may have taken place in the totality of sexually reproducing populations in evolution. I think that the occurrence may well have been frequent enough in the evolutionary time scale to produce a considerable number of successful results.

Summary

A mathematical model for the study of encounters in randomly moving particles in two dimensions is presented. This is used in connection with the mate-finding problem.

Data assembled by Stickel (1950) are analyzed and it is suggested that populations of the box turtle, *Terrapene carolina*, could maintain a population (in so far as mate-finding is concerned) at a density of as low as one per four acres without special mate-finding traits other than sperm storage.

The parameters in the random model are: reproductive time (t), activity rate (v), detecting range (r), and adult density (n), density being equal to the size of the adult population (N) divided by the geographic area involved (G). Various favorable changes in these parameters are considered. Examples are herding, use of a breeding habitat, and increased detecting at reproductive time.

Specific biological adaptations, not easily placed as directly affecting the parameters above are of two types: those affecting the problem of finding a mate, and those increasing the effectiveness of a single mating. In practice the distinction is not always clear. The efficient use of memory for example may render the use of a random model completely invalid. Sperm storage or mating for life will increase the effectiveness of a single mating.

Evolutionary implications of low density under various conditions are considered. It is concluded that natural selection could be expected to be effective frequently in sparse populations of small effective size. A possible connection between the number of rare species in the central american tropics and problems of mate-finding is noted.

It is suggested that low-density may serve as a trigger-mechanism, accelerating selection for a wide range of genotypes which at time of low-density become virtually necessary for survival because of the solution they bring to the mate-finding problem.

Acknowledgments

In preparing this paper I have become indebted to numerous persons. Discussions with F. E. Smith, University of Michigan, Pierre Dansereau, University of Montreal, and P. S. Martin, University of Arizona, have been particularly

fruitful. I am likewise grateful to Norman Hartweg, Charles F. Walker, and T. H. Hubbell of the University of Michigan. For remarks, criticism, or aid I would like to thank Alexis Zinger and Pierre Demers, respectively of the Center of Statistics and the Department of Physics of the University of Montreal, Jerome Cornfield, Office of Biometry, National Institutes of Health (Bethesda, Md.), and Sewall Wright, University of Wisconsin. D. H. Valentine, University of Durham (England), kindly criticized the manuscript. L. F. Stickel, Patuxent Research Refuge Maryland, graciously furnished original maps and data concerning turtle movement. Inclusion in the above list does not imply agreement with the contents of this paper and full responsibility for any errors herein is mine.

Appendix

The derivation of $\bar{V}_r$ for motion in two dimensions is given here. Relations in any plane triangle give

$$V_r^2 = V_1^2 + V_2^2 - 2V_1V_2 \cos \alpha$$

Since all particles move at the same velocity ($V_1 = V_2 = V$) then

$$V_r^2 = 2V^2(1 - \cos \alpha)$$

and consequently

$$V_r = 2^{\frac{1}{2}}V(1 - \cos \alpha)^{\frac{1}{2}}$$

In the above, α is the angle made between two intersecting paths of motion. Hence the mean $\bar{V}_r$ is given by

$$\bar{V}_r = \frac{1}{\pi}\int_0^{\pi} 2^{\frac{1}{2}}V(1 - \cos \alpha)^{\frac{1}{2}}d\alpha$$

or

$$\bar{V}_r = \frac{2V}{\pi}\int_0^{\pi} \sin \frac{\alpha}{2}\, d\alpha$$

giving

$$\bar{V}_r = \frac{4}{\pi}V$$

or

$$\bar{V}_r \cong 1.2732V$$

The mean relative velocity in three dimensions is much more commonly encountered because of its use in molecular physics. For a constant speed gas this is given as (cf. Kennard, 1938: 107)

$$\bar{V}_r = \frac{4}{3}V$$

or

$$\bar{V}_r \cong 1.3333V$$

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NOTES AND COMMENTS

LOONS AND THEIR WINGS

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In his interesting article on adaptive evolution in birds' wings, Savile (1957) makes several statements about the loons and their evolution which I feel require further discussion.

The idea that loons were relatives of the Upper Cretaceous Hesperornithes and are therefore primitive has persisted in the literature for many years, although in my opinion it is quite unjustified. As I have recently pointed out (1956) the best known of the early fossil loons (*Colymboides minutus*) was a small species which, compared with modern loons, had legs only moderately adapted for propulsion under water and relatively large wings, enabling it to fly strongly. Loons as we know them evolved between the time of *Colymboides minutus* (late Oligocene or early Miocene) and the Upper Middle Miocene (Calvert formation), the age of occurrence of the earliest recorded fossil of the Recent genus *Gavia* (Wetmore, 1941). Loons probably evolved from gull-like ancestors; certainly they evolved from strong-flying ones.

As has been pointed out by Stolpe (1935) and others, the similarities shared by the Hesperornithes, the grebes, and the loons result from convergent evolution. I see no valid reason for believing that they had a common swimming ancestor. The Hesperornithes were highly specialized end products of a very early adaptive radiation of birds. There is no conclusive proof that any other known Cretaceous birds possessed teeth. The retention of these structures in the Hesperornithes was of undoubted selective advantage—witness the evolution of analagous structures in the bills of mergansers. Neither the adaptive "disadvantage" of weight nor the "substitution" of a muscular gizzard discussed by Dilger (1957) as reasons for the loss of teeth in birds applied to these flightless birds which presumably used their teeth to hold their prey.

Thus loons were derived from birds which flew well, and they were not related to the Hesperornithes, which died out long before loons became their ecological counterparts. The wings of loons must therefore be thought of as either in the process of "degeneration," or as being adapted to a particular set of conditions. I would like to present evidence for the latter view.

Like the Hesperornithes and the grebes, the loons are foot-propelled diving birds. While they may swim by alternate strokes of the feet when on the surface, they move the feet simultaneously when they are below the surface. Ordinarily the wings are kept folded and under the flank feathers while the birds are under water; however, in turning sharply or when wounded or pressed, loons use their wings under water (Townsend, 1924). The speed with which loons normally move under water is indicative of the size and power of their hind limb musculature, which, compared with other birds, forms a relatively high proportion of the total body weight. Yet loons can and do perform long migrations. Thus loons appear to be adapted for sustained flight with a minimum weight of wings and pectoral muscles. An important evolutionary factor is the conservatism of wing proportions within the loons (and many other groups of birds). I have shown the remarkable similarity in the proportional lengths of the wing elements between *Colymboides minutus* and the Recent loons (1956: 415), and it is evident through what is known of their evolution that loons' wings have changed little if any in their proportions. There *has,* however, been a reduction in relative size of the fore limb as the hind limb has become increasingly heavy. What we have in modern loons is an adaptive balance; the selective advantages of an increasingly strong (and heavy) hind limb being opposed by the disadvantage of the accompanying increase in wing-loading.

Speed in flight is a compensation for a high wing-loading, and I suggest that the form of loons' wings is an adaptation for speed in flight "necessitated" by an increase in wing-loading, in turn brought about by the strong development of the legs for propulsion under water.

In using data on weights and wing areas it should be emphasized that the weights of migratory birds, and hence the corresponding figures for wing-loading, are extremely variable. I have been collecting data on the grebes and have found more than 100 per cent variation in wing-loading in the Pied-billed Grebe. Two males of this species, each having a wing area of 52 square inches, weighed 282 grams and 576 grams. The figures for wing loading are 1.75 and 3.55 pounds per square foot, respectively.

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THE LOON WING

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I regret that, in following Heilmann (The origin of birds. Witherby, London. 1926), I unwittingly perpetuated an error concerning the relationship of *Hesperornis*. I wish to thank Dr. Storer for drawing attention to this error, and I trust that his correction will be widely noted.

Dr. Storer's interpretation invalidates the chronology of my speculative interpretation of the origin of the loon wing. Whether it upsets it in other respects is a moot point. I still feel that it is quite possible that the loons arose from a line that, although capable of flight, failed to develop a really efficient wing. In particular, I find it difficult to believe that the poorly developed loon alula is anything but primitively inefficient; for, as long as a bird of substantial size flies at all, a functional alula is very valuable, and it is hard to believe that it is detrimental in swimming or diving.

I am grateful to the many correspondents who have written to me about this problem, but it must be admitted that none has yet presented a convincing alternative solution.

CROSSING RELATIONSHIPS IN THE GENUS *CARICA*

ANAND C. SAWANT

The cultivated papaya (*Carica papaya*) is native to Central America (1) and in the post-Columbus period it spread to other tropical parts of the world. Papaya cultivation is subject to serious depredations primarily from many fungus, bacteria and virus diseases. In subtropical countries, on the fringes of tropics, the papaya cannot be grown because it is very susceptible to temperatures below 40° F. Efforts are being made therefore to develop varieties resistant to diseases prevalent in the particular area, and to develop varieties for subtropical climates.

The papaya belongs to the genus *Carica*, which has some 40 species native to Central America and Northern part of South America. *C. monoica* shows some tolerance to one of the virulent papaya diseases called virus Bunchy Top, which is common in Puerto Rico and the adjoining Carribean area. *C. candamarcensis*, on the other hand, grows only at an altitude of 4,000 feet or more, which has much cooler climate for papayas. The fruit of *C. candamarcensis* is edible. The present exploratory work was undertaken, therefore, to study the crossing compatibility relations of wild species of *Carica* with cultivated papaya, a prerequisite to the transfer of any desirable characters from wild species to cultivated papaya.

Many successful, as well as unsuccessful, interspecific crosses have been reported. Warmke and others (2) reported a new interspecific cross, *C. goudotiana* × *C. monoica*, the latter being used as a male parent. Addison (3) had succeeded in making the interspecific cross, *C. papaya* × *C. monoica*. Still earlier successful crosses were made between *C. candamarcensis* × *C. papaya*, *C. cauliflora* × *C. papaya*, *C. erythrocarpa* × *C. candamarcensis*, *C. papaya* × *C. gracilis* (4). Seany and Wieland have been successful to cross *C. candamarcensis* × *C. monoica* and to study F_1 and F_2 (personal correspondence). In the present work crosses between four species, namely *C. papaya, C. monoica, C. goudotiana and C. cauliflora* were attempted.

C. papaya is a tree growing 10 to 25 feet or more. Usually unbranched, it bears large melon-

like fruits in which are found several hundred black pepper-like seeds. It has dioecious as well as hermaphroeditic forms. In the present work only dioecious forms were used.

C. monoica is typically monoecious and does not throw any off-sex types. Under Puerto Rican conditions the plant grows luxuriantly and attains 5 to 6 feet height. It grows upright and the branches shoot up right from almost every leaf axal. The stem is green but the older parts turn brown. Leaves are tri-lobed and green. Flowering starts 4½ to 5 months from the date of seed sowing. The inflorescences are borne on short stalks. Usually there is one female flower in each inflorescence but 2 or 3 female flowers per inflorescence are not uncommon. Fruits are 2½ inches long and 1½ to 2 inches wide with smooth round surface. In about 4½ months fruits ripen to deep orange color. A fruit usually has 30 well-developed seeds, although some may have as few as five to ten seeds a piece. The seeds are of a pea-size and have numerous blunt but prominent projections.

C. goudotiana: This is a typical dioecious species, no intermediate forms being encountered. It has upright unbranched stem, light purple in colour, turning with age to a dirty brown colour. The plant is usually 6 to 7 feet in height, but in good soils it attains a height of 10 feet. Leaves are borne by long purple petioles and divided into 3 to 5 lobes, each of which is again deeply subdivided to give a multiple herringbone design. The male plant flowers first in about 4½ months; and female flowers appear about a month later. The male inflorescence is a long, subdivided panicle. Female flowers are borne on short peduncle, 1 to 4 flowers per cluster. The fruit is 2 to 3 inches long and 1½ to 2 inches wide. It turns yellow after ripening in about 4½ to 5 months. Its flesh is fibrous and stringy; but is richly aromatic. The fruit is ridged and is pentagonal in cross section. A full complement normally is 50 to 80 seeds. The seeds are slightly longer than wide, and are rough on the surface.

C. cauliflora: This species also is dioecious. The stem is khaki brown and upright without branching. It is 4 to 6 feet or more in height, growing considerably slower than the other three species and appearing to be more fastidious about its soil and water requirements. The leaf lamina and the peduncle are dark green. The leaves are broad and entire with 3 to 5 pointings. Flowers, borne on short peduncles, first appear 8 to 9 months from the date of sowing. Fruits are roundish, about 2 inches long and 1¾ inches broad, with longitudinal shallow clefts. Seeds are similar to those of *C. monoica.*

Crossing Relationships

In making crosses, the following hybridization techniques were used. The fully developed female flowers of *C. papaya* are enclosed in glassine bags or the petals are tied with a piece of cotton before the flowers naturally open. On the next day these flowers are uncovered, dusted with pollen from freshly opened male flowers of the desired species and covered again with glassine bags. In *C. monoica, C. cauliflora* and *C. goudolina* the female flowers are small enough to be encased with No. 1 or 0 gelatine capsules. After being pollinated the female flowers are again covered with gelatine capsules.

C. papaya × *C. monoica:* The fruit set in this cross is 2 to 3 percent as compared to self pollination. In most cases the fruits drop within 3 or 4 weeks without any appreciable growth. Those which ripen are smaller than papaya selfed fruits and contain 10 to 15 well developed seeds apiece, only rarely having 50 or more seeds. The seeds look normal in size and appearance. Along with the normal looking seeds there is a larger number of seeds that have aborted at various stages of development and at maturity usually appear shrivelled and elongated or filled up with a watery liquid. Out of a large but unrecorded number of seeds, none germinated.

C. papaya × *C. goudolina:* In this cross the fruit set was slightly higher than the preceeding one, ranging from 3 to 4 percent. The unsuccessful crosses drop in a very early stage. The ripe fruits contain very few seeds, the germination of which was not ascertained.

C. papaya × *C. cauliflora:* This is a very unsuccessful cross and from 80 pollinations only one fruit was obtained which had 15 well developed seeds. The fruits of unsuccessful pollinations dropped in about a week. The tested seeds failed to germinate.

C. goudolina × *C. papaya:* After pollination almost every fruit developed for 2 to 2½ months, at which stage they are about ¾ of the normal size. The fruit then would turn slightly yellow at the base and drop. They had a large number of small, shrivelled seeds aborted at different stages of development. Two fruits (out of about 60 crosses), however, were fully developed after 4½ months and had a few well developed seeds. When the seeds were cleaned and dried, however, they became light and papery and failed to germinate.

C. goudotiana × *C. monoica:* In this case 15 percent of the flowers set fruit. Some of the fruits drop off as early as one month after pollination and others remain as long as 2 to 2½ months. The ripe fruit contains 10 to 15 well developed seeds along with a larger number of aborted seeds. The well developed seeds germinate poorly and slowly, the germination

TABLE 1. *Results of interspecific crosses in the genus* Carica

Cross	% Fruit set	Fruit development	Seeds per fruit	Seed condition	Germination
C. papaya × *C. monoica*	2–3	Fruits drop in 3–4 weeks	10–15	Few normal Mostly aborted	No germination
C. papaya × *C. goudotiana*	3–4	Fruits drop in 2 weeks	Few	—	Not attempted
C. papaya × *C. cauliflora*	1	Fruits drop in a week	Few	Few normal Mostly aborted	No germination
C. goudotiana × *C. papaya*	>90	Fruits drop after 2–2½ months	Few	Light, papery aborted	No germination
C. goudotiana × *C. monoica*	15	Fruits drop after 1–2½ months	10–15	Few normal + many aborted	5% germination slow
C. goudotiana × *C. cauliflora*	5–6	Fruits drop after 3–4 weeks and after 2–3 months	Very few	Small, shrivelled and aborted	—
C. monoica × *C. papaya*	6–7	Fruits drop in 1–2 weeks	3–4	Normal looking	No germination
C. monoica × *C. papaya*	>90	Normal	Many	Normal looking	Not attempted
C. monoica × *C. cauliflora*	50–60	Few drop in 1–2 weeks	10–20	Variable size	10–15%
C. cauliflora × *C. monoica*	Nil	—	—	—	—

being as low as 5 percent. The seedlings are weak in the beginning but later they recover and make normal growth.

C. goudotiana × *C. cauliflora:* As in the case of *C. goudotiana* × *C. monoica* some fruits develop for 3 to 4 weeks and then drop. More than half the fruits, however, continue their normal growth for 2 to 2½ months or even 3 months before abscission. Only 5 to 6 percent of the fruits come to maturity after 4½ to 5 months and contain small shrivelled seeds. The few normal looking seeds dried to a light and papery condition, and failed to germinate.

C. monoica × *C. papaya:* More than 50 percent of the pollinated flowers drop in the first week after pollination, while others develop into small fruits about ⅕ normal size. Only three fruits out of 42 pollinations were well developed and contained 3 or 4 seeds apiece. The seeds failed to germinate. For a different trial two *monoica* plants were planted in the midst of plantations of *C. papaya.* There were no other species in a radius of a few miles. The male flowers from *C. monoica* were removed in early stage so that the only pollen that could reach *C. monoica* pistilate flowers was from *C. papaya.* These plants had normal fruit set and the fruits had many full-size seeds.

C. monoica × *C. cauliflora:* This was the most successful cross, 50 to 60 percent of the pollinations producing mature fruits of normal size. In unsuccessful cases the fruit usually dropped within a week or two, but in a few cases the small undeveloped fruit would hang on until it ripened to natural color; but not containing any seed. Each well developed fruit had 10 to 20 seeds of variable size and development. The germination was between 10 and 15 percent. The seedlings were healthy and vigorous, showing great hybrid vigour and transgressive inheritance over both the parents.

C. cauliflora × *C. monoica:* All attempts to make this cross have met with failure. The pollinated flowers dropped off within a week. Application of .001 percent indolebutyric acid in lanolin to pedicels of female flowers was tried without any success.

DISCUSSION

The results of these crosses, though not very extensive, are fairly enough indicative of the affinities and the barriers between these species. There seems to be a greater success in crosses between *C. monoica* and *C. cauliflora* only when the former is used as female indicating a closer relationship. This relationship, however, is broken down by low seed set and low germination of hybrid seeds. This affinity is completely negated by a strong isolation barrier in the reciprocal cross where the cross pollinated flowers dropped within a week. This difference in crossabilities is seen in all reciprocal crosses of these species.

These tests also show the isolation barrier between different species in operating at different stages. In *C. cauliflora* × *C. monoica* the fruit drops within a week indicating the pollen probably does not reach the ovule. When *C. goudotiana* on the other hand is used as the female parent with all other three species as male parents the fruits hold on as late as 2½ months or later and seeds develop to a considerable extent. Here the barrier operates through the disharmonious growth of embryo and the endosperm. Still, in others, the breakdown occurs in F_1 seeds either by their poor germination or/and by week plants. The study of degree and stage at which the isolation barrier operates combined with the geographic distribution of the species may reveal the precise correlations between these species.

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COMMENTS ON THE ORIGIN AND PHYLOGENY OF THE ANGIOSPERMS

M. G. POPOV (posthumous) AND G. L. STEBBINS

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A few months ago, I received a letter from Dr. A. A. Yatsenko-Khmelevsky of Tiflis, USSR, calling my attention to a posthumous article by M. G. Popov in the "Botanicheskii Zhurnal," in which reference was made to statements by Dr. Edgar Anderson and myself concerning the role of hybridization in the origin and early evolution of the angiosperms, and asking me if Dr. Anderson and I had been correctly interpreted. In reply, I sent an extended discussion of my opinion on this topic, which Dr. Yatsenko-Khmelevsky asked permission to translate into Russian and publish in the "Botanicheskii Zhurnal." I then felt that the material might also be of interest to American readers, and so suggested publishing it in EVOLUTION, a suggestion to which Dr. Yatsenko-Khmelevsky agreed. The discussion, however, would not be complete for the readers of EVOLUTION without a translation of Popov's original article, which is, therefore, included also:

ESSAY ON THE ORIGIN OF ANGIOSPERMS

M. G. POPOV (posthumous)

Botanicheskii Zhurnal 41: 768–769

When I published my article "Systematics of the angiosperms in connection with the problem of their evolution" (Popov, Bot. Zhurn. 1954, 6), I did not know about the small note by Anderson (1934), "Origin of the angiosperms." This note is full of deep understanding and significance. Studying the family Magnoliaceae, the author called attention to the fact that it and related families have the unusual chromosome number, 19, and that at the same time they represent different transitional forms between gymnosperms and angiosperms. Being a proponent of the theory of hybridization as a source of new types, Anderson naturally arrived at the opinion that all of these families arose as polyploid hybrids, as a result of crosses between cycads ($n = 12$) and Gnetales ($n = 7$). It is probable, he concluded, that all angiosperms arose in this fashion.

I first learned about Anderson's idea in 1955 from the work of Cronquist, "Phylogeny and taxonomy of the Compositae," in which the author referred with some sympathy to Anderson's hypothesis, calling it at the same time bizarre and not ordinarily acceptable. However he cited here also Stebbins (1950), who actually expresses a similar idea on the rapid and simultaneous development of all of the angiosperm families as a result of polyploidy and hybridization of some "ancestral types."

There is no doubt about the priority of Anderson for this idea about the origin of angiosperms. This idea is absolutely correct, although its opponents might not say so.

Here I should like to call attention only to the fact that one and the same basic idea on the origin of the angiosperms arose completely independently in two separate continents and in the minds of two investigators of very different background; one derived from a cytological and the other from a morphological basis. Therefore, if people maintain one principal viewpoint, that is, to recognize hybridization as a basic factor in the origin of new types, then, if they are neither committed to or preoccupied with one side of the question, they necessarily arrive at one and the same, the only possible conclusion, that the angiosperms represent hybrid polyploids from crosses of Gnetales and Bennettitales (Cycad-like types).

Now I should like to answer my eminent critic, A. A. Yatsenko-Khmelevsky (1955). In his opinion, hybridization between categories higher than genera is completely impossible, and he thinks that according to this principle all our conceptions about the hybrid origin of angiosperms are altogether without probability. A. A. Yatsenko-Khmelevsky derives his basic affirmation from the results of human experiments. To us such an experiment does not appear decisive. Human experiments in relation to nature's experiments are of a very small scope, almost approaching nothing. Nature operates with hundreds of thousands of species, with billions of individuals in the course of millions of years, on huge areas of all lands. We therefore introduce the factor of time into the evolutionary process, but in a different way from that of the orthodox Darwinians. In our opinion, any crossing is possible in nature, but its probability is limited by time. We can say in general that the more distantly two systematic categories are related to each other, the lower is the probability of crossing between them in nature, that is, the greater is the interval of time between occurrences of hybridization. Crossing between families requires millions of years, crossing between classes requires tens of millions of years. I speak of productive hybridization, which leaves descendants in the form of definite systematic categories.

The great event, the birth of the angiosperms, that is, crossing between the Gnetales and the Bennettitales, was being prepared during millions of years, then was accomplished in our human point of view "purely accidentally," apparently only in one spot on the earth and only once. It is useless to affirm that it is impossible; it is possible only to say that statistically it is very improbable; that is millions of years were required for it to take place.

No other solution of the problem of the origin of the angiosperms appears possible. No other point of view, other than hybridization, appears favorable for solving the problem of actual evolution, evolution in the course of time, that is, that evolution which actually took place on the earth, in definite zones, regions, and definite geological epochs.

My critic says that I do not produce any examples of secondary and tertiary hybridization; I simply declare it as so. In this matter all of my conceptions on the origin and development of the ancient Mediterranean flora, with its thousands of genera and tens of thousands of species, even with some endemic secondary families, represents a real example of the fact that secondary repeated hybridization, determined by the course of geological events and depending on the consequent migration of floras, yielded in a short section of time a great new flora. Consequently the history of the ancient-Mediterranean flora was the initial basis from which my general theory of the hybrid origin of the angiosperms was developed. In its later stage, it came into complete agreement with the opinions which independently and on the basis of completely different material, in part caryological, were developed by the American botanists Anderson and Stebbins. Whatever our critics might say, it is clear to us that the basic problem of the origin of the angiosperms is solved, and that nobody can proceed anywhere away from this solution. It will not capitulate because of difficulties, as A. A. Yatsenko-Khmelevsky thinks, this—the solution of the problem. No "integral phylogeny" can here change anything basically. . . .[1]

Translated by G. L. Stebbins
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[1] M. G. Popov died without having finished this article. Nevertheless, the editors of the "Botanicheskii Zhurnal" consider it necessary to publish it in memory of the author—an outstanding botanist.

ON THE HYBRID ORIGIN OF THE ANGIOSPERMS

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In a recent discussion between Dr. A. A. Yatsenko-Khmelevsky and the late Dr. M. G. Popov on the origin of the angiosperms by means of hybridization between different groups of gymnosperms, the latter author (Popov, 1956) referred to my opinion on this subject, as expressed in my book, "Variation and Evolution in Plants." Dr. Yatsenko-Khmelevsky (in

litt.) has recently called my attention to this discussion, and has asked me to clarify my stand with regard to it. This is the purpose of the present article. I am most grateful to Dr. Yatsenko-Khmelevsky for giving me this opportunity, and for his kind assistance in translating the article into the Russian language.

My position on this point has been expressed on pages 363–365 of my book. I refer to the hypothesis of Anderson (1934), which was accepted also by Popov, namely that the angiosperms might have originated from hybridization and allopolyploidy between ancestral types of conifers or Ginkgoales and ancestral Gnetales, as follows: "On grounds of external morphology, this suggestion is so highly improbable as to be hardly worthy of serious consideration." I still hold this opinion. In fairness to Dr. Anderson, the point must be emphasized that he did not conceive of this hybridization as taking place between types corresponding to modern conifers and gnetales, as Popov apparently did. The ancestral types which he had in mind were completely extinct genera or families which were related to the modern forms and resembled them in chromosome number.

On the other hand, I presented evidence from chromosome numbers in the woody Ranales to support my hypothesis that the original basic numbers in this order were $x = 6$ and $x = 7$, and therefore that the basic number $x = 19$, which is so widespread in it, was derived by allopolyploidy between different subgenera or at most between genera of Ranales. One further bit of evidence has appeared recently, namely the discovery by Mr. Roman Gankin, a student in the Botany laboratory of this University, that *Drimys lanceolata,* an Australian species, has the somatic number $2n = 26$ ($x = 13$). This suggests that both the numbers $x = 7$ and $x = 6$ may have existed originally in the family Winteraceae.

Although I cannot accept the hypothesis that the angiosperms originated by allopolyploidy involving different orders of gymnosperms, I nevertheless believe, as I stated on page 365 of my book, that allopolyploidy was involved in the evolution of families within the class of angiosperms. In stating this belief, however, I wish to make clear the fact that I do not believe that new families can arise from hybridization between species belonging to families which are well differentiated and widely separated from each other. On the other hand, we must remember that most families of angiosperms originated a long time ago, probably in the Cretaceous period. At that time, there may very well have existed many examples of closely related genera or subgenera which differed from each other in respect of characters which we now associate with the differentiation of families or orders, such as choripetaly vs. sympetaly, hypogyny or perigyny vs. epigyny, and many vs. one carpel per flower. Even today there exist families or genera which have variability with respect of one of these characteristics, such as the Liliaceae (choripetaly-sympetaly), *Saxifraga* (perigyny-epigyny) and *Delphinium* (many-one carpel per flower).

Consideration of these facts should help to clarify my statement that (1950, p. 365) "students of angiosperm phylogeny should look for traces of ancient allopolyploidy resulting from hybridization between species which were the ancestral prototypes of many of our modern families." By "ancestral prototypes" I mean species which differed from each other in respect of many characteristics which now differentiate certain modern families, and which were actually ancestral to these families, but which at that time in the remote past had not become any more strongly differentiated from each other genetically than are members of different genera or subgenera of modern times. Two examples will serve to illustrate my point.

The origin of the large series of sympetalous groups placed by Engler in the Gentianales and Polemoniales, and by other authors in the Contortae and Tubiflorae, has been conceived very differently by various modern students of angiosperm phylogeny. Bessey (1915) and Hutchinson (1926) considered them to be derived from the Caryophyllales, Gobi (1916) and Grossheim (1945) from the Rosales, Soo (1953) from the Geraniales, and Takhtadjian (1954) from the Rosales via a common ancestor with the Celastrales. These differences of opinion may result from the fact that no one of these modern orders was exclusively responsible for the origin of the Contortae and Tubiflorae. Instead, the latter orders may have originated by hybridization and allopolyploidy between one species which possessed certain morphological characteristics of the Geraniales or Celastrales and another species which possessed certain characteristics of the modern Rosales. But these two ancestral species by no means resembled any modern genus of Geraniales, Celastrales, or Rosales, except in a few particular diagnostic characteristics. Furthermore, they probably had as close a genetic relationship to each other as do two neighboring modern genera belonging to one of these families.

A second example is my interpretation of the origin of the subfamily Pomoideae of the Rosaceae. In my book (1950, p. 361), I suggested that the original members of this tribe, which has the basic chromosome number $x = 17$, "arose as amphidiploids between primitive or ancestral members of the tribes Spiraeoideae and Prunoideae." I do not mean by this statement that, for instance, a member of the modern genus *Spiraea* was able to cross with a species belonging to the modern *Prunus.* Such a cross

would be completely impossible, not just very highly improbable, as Popov has suggested. In the Cretaceous period, however, there probably existed genera of Spiraeoideae and Prunoideae which were entirely different from modern genera, and much more closely related to each other. Evidence for this hypothesis is presented by the existence of certain relic genera of both tribes which resemble both the Pomoideae and each other more strongly than do the dominant genera of modern times. The genus of Spiraeoideae which resembles most closely the Pomoideae is *Vauquelinia,* a small genus found in the southwestern United States and adjacent Mexico, which in all characteristics except its gynaecia and fruits bears a strong resemblance to *Photinia* and *Heteromeles* of the Pomoideae. In the Prunoideae, two genera should be considered. One is the monotypic *Osmaronia,* of western North America, and the other is *Exochorda,* a monotypic genus of China. These two genera differ from *Prunus* and resemble most of the Pomoideae in having five carpels per ovary, as does also *Vauquelinia. Osmaronia,* however, is specialized in a direction peculiar to itself, since it is dioecious. *Exochorda,* on the other hand, is a possible living link between the tribes Spiraeoideae and Prunoideae. Although placed by most authors in the Spiraeoideae on the basis of superficial morphological features, it was placed in the Prunoideae by Juel (1918) on the basis of the position of its ovules, and it agrees with the Prunoideae in having the basic chromosome number $x = 8$. The three genera mentioned (*Vauquelinia, Osmaronia, Exochorda*) are all very distinct not only from each other but also from all other genera of Rosaceae. Furthermore they are much reduced in number of species, widely separated from each other in geographic distribution, and except for *Exochorda* they occur in regions far removed from the place where the Pomoideae probably originated, which is central Asia. Along with other primitive, isolated genera of Rosaceae, such as *Kageneckia* and *Quillaja* of South America, they are probably the last relics of an ancient complex of genera, which were more numerous, widespread, and richer in species at some time in the past. At that time, which may have been the Cretaceous period, there could have been several types like the modern *Exochorda,* which were transitional between Spiraeoideae and Prunoideae as we now know them, and from hybridization between such types the first members of the Pomoideae could have arisen.

The objection may be raised that this hypothesis assumes the past existence of too large a number of species and genera which are now extinct. Because of the nature of preservation of angiosperm fossils, which consist mostly of leaves, we have no way of knowing how many completely different floral types existed in the past. But even in the Eocene London Clay flora (Reid and Chandler 1933), a large number of the fossil flowers and fruits cannot be placed in modern genera. In the conifers, which have a much better fossil record than the angiosperms, Florin (1944) has shown that the interrelationships between modern genera can be understood only by taking into account the large number of extinct, Permian genera, which had fructifications entirely different from those of modern conifers. Even better examples can be found in the fossil record of animals, particularly the vertebrates. They show us that modern forms are nearly all ends of evolutionary lines which have at least a few specialized characteristics, and that no phylogenetic tree erected on the exclusive basis of living genera and species can come even close to expressing the true relationships between these genera. To understand the ancestry of and therefore the evolutionary connections between modern genera and families, we must know something about extinct fossil forms.

Because of this fact, and also because of the possibility that in its early stages the phylogeny of the angiosperms may have been highly reticulate, I believe that no phylogenetic tree which can be constructed on the basis of present day knowledge can express the genetic interrelationships between orders and families of angiosperms with any degree of accuracy. This is an embarrassing situation for the student of angiosperm evolution, but it must be faced honestly and in a realistic fashion. Only in this way can we expect to learn more about how the flowering plants evolved.

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THE GEOGRAPHICAL DISTRIBUTION OF VERTEBRATES[1]

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To be perfectly frank, this review is an open fan letter to Philip J. Darlington, Jr. In my opinion his Zoogeography is one of the several really important books on or about evolution that have appeared within the last decade. The book is restricted to the analysis of the patterns of distribution of terrestrial and fresh water vetebrates. The fact that Darlington is himself a specialist on carabid beetles particularly qualifies him for the awful task he has assumed. He can look at vertebrate distributions as a zoogeographer and not as a systematist unconsciously anxious to demonstrate the inherent value of a special group of animals. That is not to say that he is without a distinctive point of view. On the contrary, this is an intensely personal book, but he takes great care to distinguish between that which is Darlington and that which is evidence. It is an honest book. When he feels that the evidence is good but not conclusive he writes "probably." When he means to say "I think . . ." that is what he says. In his introduction he describes his working tools and then writes on to describe their weaknesses. Such candor in our literature is impressive if not even frightening.

In the beginning of the book Darlington poses four questions:

1. "What is the main pattern of animal distribution?"
2. "How has the pattern been formed?"
3. "Why has the pattern been formed?"
4. "What does animal distribution tell us about ancient lands and climates?"

In 675 pages of well written and illustrated text he reassesses the facts of vertebrate distribution and relates them to these questions. The work consists of two parts. In the first of these Darlington summarizes the data for each class of vertebrates. The latter portion of the book is devoted to a synthesis of this evidence and the formulation of major conclusions.

Darlington discusses the geographic distribution of each class under the headings: classification, fossil record, limits of distribution, regional distribution, transitions and barriers in distribution, dominance and competition, patterns and history of dispersal. One of the many difficulties in attempting a zoogeography on this scale is that it is virtually impossible to show the reader the raw data. Darlington reduces the amount of faith required by the use of examples of the kinds of data employed and by basing his conclusions, as much as possible, on the evidence summarized in the lists of families following each systematic chapter. Following the detailed discussions of each of the classes of vertebrates is a chapter summarizing continental patterns. On the basis of the combined patterns of distribution, the division of the world into faunal regions is attempted. The result is a familiar system in an unfamiliar context. The divisions are represented as an average pattern, not a common one. The system is coolly defended as a real and significant way to show how animal distribution "is fitted to the world" without, at the same time, minimizing the underlying complexity. The next chapter on island patterns will be of interest to geologists as well as biologists. Among several conclusions, he found that most island vertebrates are recent immigrants and not ancient relics.

The climax of his book is reached in chapter 9 entitled "Evolution of the geographical patterns; area, climate and evolution." Within this chapter he brings together all of his previous conclusions and tries to weave them together in general hypotheses. He concludes that the main pattern of dispersal of vertebrates has been "from the largest and most favorable areas, especially from the main part of the Old

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[1] Zoogeography: The Geographical Distribution of Animals, by Philip J. Darlington, Jr. 1957. John Wiley & Sons, New York. 675 pages, 80 figures, 21 tables. $15.00.

World tropics into smaller and less favorable areas." The terrestrial and fresh water vertebrates seem to have dispersed from the tropics into the north-temperate zone more than the reverse as was argued by Matthew. Darlington discerns three major routes of dispersal; from the Old World tropics to temperate South Africa, from Tropical Asia to Australia and New Zealand, from the Old World tropics through temperate Eurasia and North America to tropical Central and South America.

In a chapter on the zoogeography of the past he adds that "As far back as the record goes, in spite of all doubts, the distribution of animals can be reconciled with a pattern of land and climate like the present one." Not content to show that many of the proposed land bridges are not necessary, he produces evidence to show that they are indeed highly improbable. He ends the chapter weakly with an unnecessary and detracting hypothetical history of the continents. In the final chapter Darlington attempts to apply principles of zoogeography to the geographic history of man. I do not think he demonstrated any advantage for this approach to man's history.

All in all, Darlington reaches a conservative position regarding the major features of vertebrate distribution. Taken separately, his main conclusions are not novel. What makes this book really significant is the overwhelming evidence he has brought up in defense of this arrangement of ideas. He has arrived at his strong position from a careful reappraisal of all the facts available. He has done so without producing a dogmatic impediment to further research. Indeed, to many his book will introduce the idea that objective research in zoogeography is possible and profitable.